Universidade de Aveiro Departamento de Biologia
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CAMILO ANDRÉ FERREIRA CARNEIRO

ENTRE O ÁRTICO E OS TRÓPICOS: IMPLICAÇÕES DAS MIGRAÇÕES DE LONGA DISTÂNCIA NA QUALIDADE INDIVIDUAL

BRIDGING FROM THE ARCTIC TO THE TROPICS: IMPLICATIONS OF LONG-DISTANCE MIGRATION TO INDIVIDUAL FITNESS

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Tese apresentada à Universidade de Aveiro para cumprimento dos requisitos necessários à obtenção do grau de Doutor em Biologia, realizada sob a orientação científica do Doutor José Augusto Belchior Alves, Investigador Auxiliar e Professor Auxiliar Convidado do Departamento de Biologia da Universidade de Aveiro, e co-orientação do Doutor Tómas Grétar Gunnarsson, Research Professor da Universidade da Islândia

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“I believe that I myself am not at all insensitive to an animal’s beauty, but I must stress that my aesthetic sense has been even more satisfied since I studied the function and significance of this beauty.” Niko Tinbergen, *Curious Naturalists*, 1958.

o júri

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Doutor José Augusto Belchior Alves
Investigador Doutorado, Universidade de Aveiro

agradecimentos

When I started this PhD, I remember José telling me that it could be a lonely road. I believe he meant it as an advice, in case I would need to surround myself with people. I thought I would be fine, and I made no effort to have people around and avoid that possible loneliness. The fact is that as I sit down to write these acknowledgements and look back, what I mostly see are people and the good times I spent with them, not the science itself. Without directed effort, I naturally met many people during the last four years, mostly at conferences (to attend them was another advice José gave me early on), and all those, alongside old and new friends, made it a great journey.

I am very grateful to José and Tómas for taking the responsibility of supervising me, but mostly for their friendship and enthusiasm on this project. I learnt a lot from them and fully appreciate all the discussions, which sharpened my critical thinking.

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And Triin Kaasiku, for making the final stages of this journey much easier. Tänan sind.

palavras-chave

fenologia, reprodução, migração, invernada, efeitos *carry-over*, ciclo anual, efeito domino, *trade-off*, repetibilidade, consistência, maçarico-galego, *Numenius phaeopus.*

resumo

Para muitas espécies as alterações climáticas ocorrem mais rápido do que a sua capacidade de resposta e a situação pode tornar-se mais complicada no árctico e sub-árctico, onde as temperaturas têm aumentado de forma mais célere do que a latitudes inferiores. Isto é particularmente problemático para migradores que usam várias regiões climáticas durante o seu ciclo anual. De facto, vários migradores de longa distância estão em declínio global e para perceber a sua capacidade de resposta a nível populacional, é primeiro necessário compreender como os processos que ocorrem ao nível dos indivíduos podem influenciar o seu *fitness*.

Os maçaricos-galegos da subespécie islandesa *Numenius phaeopus islandicus* proporcionam um bom sistema de estudo para investigar estas questões. Nesta tese investiguei (1) as diferenças sazonais na duração da migração, velocidade de migração e velocidade do voo em relação ao solo, e mapeei as rotas de migração, zonas de invernada e de paragem migratória desta população; (2) examinei *trade-offs* energéticos à escala da distribuição da população e os potenciais efeitos de *carry-over* das condições de invernada no período de reprodução; (3) determinei a variação sazonal e sexual na consistência do *timing* individual ao longo do ciclo anual; (4) usando dados a nível individual para todo o ciclo anual, investiguei correlações entre estádios anuais e a duração de períodos estacionários, e avaliei as suas consequências no *fitness* individual; e (5) explorei como as condições de vento, temperatura e data de saída durante a migração influenciam a estratégia migratória primaveril.

Ao contrário da maioria dos migradores sazonais, os maçaricos-galegos islandeses tendem a migrar mais rápido no outono do que na primavera, e durante a migração primaveril a estratégia de *stopover* é mais comum. Descrevi *trade-offs* entre a distância de migração e a qualidade do local de invernada, mas invernar num local de maior qualidade aparentemente não tem influência na fenologia de reprodução ou investimento reprodutor. Assim, depois de estabelecer que o sucesso reprodutor decresce com a data de postura, o local de invernada não parece ter consequências no *fitness* individual. Demonstrei que os indivíduos são consistentes no calendário anual, principalmente na data de saída na migração primaveril. Ainda assim, ocorrem ajustes ao calendário durante períodos estacionários (e.g. *stopover*, invernada), o que permite evitar ou atenuar implicações negativas entre épocas reprodutoras, ao compensar atrasos e nidificar a tempo. Contudo, entre estádios consecutivos do ciclo anual a compensação parece insuficiente. A estratégia usada na migração primaveral não teve uma influência clara na data de postura (portanto é improvável que afecte o *fitness* individual) e não parece depender das condições de vento. Indivíduos que partem mais tarde, tendem a fazer um voo directo para a Islândia e chegar antes daqueles que fazem uma paragem migratória.

resumo (cont.)

Como em outras espécies, o *timing* é crucial para os maçaricos-galegos islandeses, particularmente a data de postura, que influencia o sucesso reprodutor. Apenas encontrei um efeito significativo da data de chegada na migração primaveril na data de postura (no entanto, a data de chegada pode ser influenciada por outros factores). Os efeitos da disponibilidade alimentar e condições atmosféricas nos locais de reprodução, e a relação entre os membros do casal não foram investigados, mas é discutido como podem influenciar a data de postura. Adicionalmente, sugiro que o declínio no sucesso reprodutor com a data de postura é provavelmente causado por pressão de predação nas famílias de maçaricos-galegos.

Uma vez que os indivíduos são consistentes no calendário e o *timing* é crucial, é importante adquirir conhecimento (i) sobre a dinâmica de recursos alimentares nas áreas de reprodução, para compreender em detalhe como esse factor pode vir a tornar-se limitante, dado o cenário actual de alterações ambientais; e (ii) sobre a ontogenia de migração e *timing* associado, uma vez que permitirá entender como o *timing* de migração é estabelecido e prever respostas populacionais.

keywords

phenology, breeding, migration, non-breeding, carry-over effects, annual cycle, domino effects, trade-off, repeatability, consistency, whimbrel, *Numenius phaeopus*.

abstract

Climate is changing at a faster pace than some species can adjust to and the situation can become more complicated in the arctic and sub-arctic, where temperatures are warming more rapidly than at lower latitudes. This can be particularly problematic for long-distance migrants using multiple climatic zones during the annual cycle. In fact, several long-distance migrants are in decline globally and in order to unravel population level responses it is essential to first understand how processes operating at the individual level can influence fitness. Icelandic whimbrels *Numenius phaeopus islandicus* provide a suitable system in which to investigate these questions. I investigated (1) differences in seasonal migration duration, speed and ground speed, and mapped migration routes, wintering and stopover; (2) examined range wide energetic trade-offs and associated carry-over effects of wintering area conditions into the breeding season; (3) explored seasonal and sex-specific variation in consistency of individual timing during the annual cycle; (4) using full annual cycle individual level data, I investigated correlations between annual stages and duration of stationary periods, and assessed their fitness consequences; and (5) explored how wind conditions, temperature and departure date influence spring migratory strategy of Icelandic whimbrels.

Contrary to most seasonal migrants, Icelandic whimbrels tended to migrate faster in autumn than in spring, and during the latter migration period a stopover strategy was prevalent. I found a trade-off between migration distance and wintering site quality but spending the winter at higher quality sites had no apparent influence on breeding phenology or breeding investment. Hence, after establishing that fledging success decreases with laying date, fitness consequences did not seem to emerge from winter site use. I also show that individuals have consistent schedules during the annual cycle, particularly at spring migration departure. Yet, schedule adjustments seem to occur during stationary periods (e.g. stopover, wintering), which likely allow whimbrels to avoid or alleviate negative fitness consequences between breeding seasons, by compensating for delays and breed on time; however, compensation between consecutive stages within the annual cycle is insufficient. The migratory strategy used in spring had no clear influence on laying date (hence unlikely to influence fledging success) and did not seem to be driven by wind conditions. Instead, individuals departing later tended to fly directly to Iceland and arrive earlier than those that stopover.

abstract (cont.)

As in other systems, timing is crucial for Icelandic whimbrels, particularly laying date, which links to breeding success. I only found a significant effect of spring arrival date on laying date (although spring arrival can be influenced by other factors). Variables such as food supply and weather conditions in the breeding area and pair bond were not investigated, but I discuss how these might influence laying date. Additionally, I suggest that the decline in fledging success with laying date is likely caused by predation pressure on whimbrel broods.
Since individuals are consistent in phenology and timing is crucial, it is important to acquire knowledge (i) on food resource dynamics at the breeding areas, to comprehend in detail how these may become limiting under a scenario of environmental change; and (ii) on the ontogeny of migration and associated timing, as this allow to understand how migratory schedules are defined and forecast population-level responses.

CONTENTS

CHAPTER 1

INTRODUCTION

Previous photo by Hugo Lousa.
Icelandic whimbrel, Iceland, 24 June 2017.
The Icelandic population of whimbrels is estimated to be 256000 pairs.

INTRODUCTION

Every year, millions of birds fly hundreds to thousands of kilometres, over oceans, deserts and high mountains in order to move between the breeding and non-breeding sites (Newton 2007). Migration is a fundamental period and one of the most energetically costlier life-history events in the annual cycle of avian migrants, alongside breeding and moult. The sequential events that compose the annual cycle can vary in space and/or time, depending for example on where and when the moult of feathers is performed (e.g. in the breeding or the wintering grounds; Newton 2011). Nevertheless, four main periods can typically be recognized in the year of seasonal migrants - breeding, autumn migration, wintering and spring migration – and throughout these, several stages can be defined (e.g. departure and arrival dates during migration, laying date, stopover periods; Fig. 1.1).

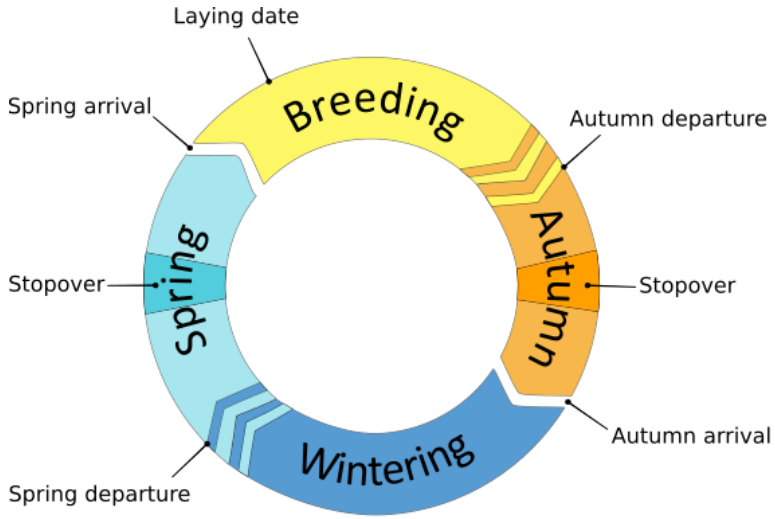


Figure 1.1. Annual cycle of a typical seasonal migratory bird, showing the four main periods (breeding, autumn migration, wintering and spring migration) and several stages (departure and arrival dates during migration, laying date, stopover periods; note that the number of stopovers during migration encompasses considerable variation among species).

Timing of breeding

The timing of breeding is important because it can influence breeding success (Perrins 1970, Drent 2006, Morrison et al. 2019). However, due to the sequential and cyclical nature of the annual events, timing of breeding is not totally independent. It also depends on the timing of the previous stage, which can in turn vary with earlier events, possibly in a series of timing correlations. Hence, if individuals incur a delay in any stage of the cycle, a 'domino effect' may arise and influence breeding performance later in the year by means of carry-over effects (e.g. Saino et al. 2017, Gow et al. 2019). However, while a domino effect may be expected and difficult to overcome during sequential movement stages, at stationary locations (e.g. migratory stopover or wintering) individuals might have the opportunity to adjust their schedule, compensate for delays and perform the following stage

"on time" (Conklin and Battley 2012, Senner et al. 2014, Briedis et al. 2018). For example, great snipes *Gallinago media* tend to spend shorter periods in the wintering areas after a late arrival and individuals that leave later on spring migration have shorter stopover durations during their return to the breeding sites (Lindström et al. 2016).

Wintering conditions

After breeding, seasonal migrants travel to a site (or sites) where they will spend the winter period until the following spring (pre-nuptial) migration. Wintering distribution can span over wide geographical ranges and distinct climatic regions. Hence, among wintering sites, weather conditions (Castro et al. 1992), habitat and food availability and quality (Piersma et al. 1993, Marra and Holmes 2001, Mathot et al. 2007) will vary, potentially creating distinct costs and benefits for individuals in different sites and thus experiencing different trade-offs (Alves et al. 2013). Spending the winter at a good site can therefore be beneficial, for example if it allows for higher intake rates, that may lead to faster fuelling during migration, when compared to suboptimal sites (Aharon-Rotman et al. 2016).

Migration

Migration is comprised by stationary fuelling periods, when energy is deposited, and by migratory flights, when energy is consumed and distance is covered (Alerstam and Lindström 1990, Lindström et al. 2019). Fuel deposition is a much slower process than energy expenditure, hence fuelling periods typically represent the larger proportion of migration (Hedenstrom and Alerstam 1997). The amount of fuel deposited can vary with migratory strategy, as individuals may optimize one of three important currencies: energy, time and/or safety (Alerstam and Lindström 1990). Such optimization may also be reflected, for example, in the number and length of stopovers and distance covered.

The interspecific variation in migration distance and number of stopovers is substantial, as while some species migrate few hundred kilometres between the breeding and wintering sites, others cover several thousand kilometres; some make a series of stopovers intercalated with relatively short flights and others make long flights with very few stops (Piersma 1987, Newton 2007). Many waders are long-distance migrants and can exhibit extreme migrations, as they cross inhospitable regions, flying continuously during several days in very long flights (Lindström et al. 2016, Alves et al. 2016, Conklin et al. 2017). Variation in migration distance can also occur at the population level, as among conspecifics breeding in the same area, differences in migration distance can be considerable. For example, sanderlings *Calidris alba* breeding in proximity in Greenland can winter from the coasts of the North Sea to southern Africa, with inter-individual migration distance differing by thousands of kilometres (Reneerkens et al. 2009). Even at the individual level, during a birds' lifetime, migratory strategies can vary. One example are sharp-tailed sandpipers *C. acuminata*, in which most juveniles migrate ca. 2300 km from the birthplace in eastern Siberia to western Alaska and from there make

an apparent non-stop flight over the Pacific Ocean to the wintering sites in Australia, while most adults migrate via east Asia, largely overland (Handel and Gill 2010, Lindström et al. 2011).

As most birds travel through the air, weather conditions are often taken into consideration in the context of migration, and wind and temperature have been shown to influence migration at different stages and in different ways (Shamoun-Baranes et al. 2017). For example, wind conditions during flight can extend the length of migration (Gill et al. 2014a) and force individuals to stop (Shamoun-Baranes et al. 2010), and temperature has been shown to influence individuals' flight altitude (Senner et al. 2018). At departure from stopover sites, individuals may select favourable wind directions (Schaub et al. 2004, Gill et al. 2014a) or depart irrespectively of that (Alerstam et al. 2011), while temperature can also affect the decision of when to leave (Berchtold et al. 2017).

Trade-offs, carry-over effects and fitness consequences

Trade-offs are ubiquitous in nature, with individuals allocating time or energy to a given activity at the expense of another, thus balancing conflicting requirements in order to maximise their fitness. For example, Icelandic black-tailed godwits *Limosa limosa islandica* trade-off longer distances of migration (and costs) to Iberia with better foraging opportunities and lower thermoregulatory costs in this region during the winter, in contrast to flying shorter distances to Britain and endure harsher wintering conditions (Alves et al. 2013). The decision to spend the winter at an optimal or suboptimal site is not trivial even if it has no survival costs, because it can influence individuals' fitness later in the annual cycle during the breeding season (Alves et al. 2013).

Carry-over effects arise when "an individual's previous history and experience explains their current performance in a given situation" (O'Connor et al. 2014; see also Harrison et al. 2011). These effects can occur over distinct temporal scales, have a reversible character ('reversible state effects' *sensu* Senner et al. 2015), and have fitness implications. For example, in the case of Icelandic black-tailed godwits, birds wintering in higher quality sites in Portugal tend to have earlier arrival dates into Iceland in the following spring, compared to conspecifics wintering in Britain (Alves et al. 2013). This allows them to occupy higher quality breeding territories (Gunnarsson et al. 2005, Alves et al. 2013), and likely start nesting earlier, thus increasing their chances of breeding successfully as timing of breeding if often positively correlated to fledging success (Bêty et al. 2004, Norris et al. 2004, Sergio et al. 2007, Alves et al. 2019). In Cory's Shearwaters *Calonectris diomedea*, carry-over effects can persist from one breeding season to the next, as the breeding investment in one season influences the subsequent schedule and migratory strategy of individuals (Catry et al. 2013). Birds that failed breeding, departed from the wintering locations earlier in the following year and arrived at the breeding colony earlier, which influenced their probability of breeding (Catry et al. 2013). Carry-over effects may also arise through a more direct influence of external factors, such as weather experienced during migration. For example, it was reported for yellow warblers *Setophaga petechia* that wind conditions experienced during spring migration had an effect on timing of breeding and

annual productivity (Drake et al. 2014). Carry-over effects can therefore be initiated at different stages of the annual cycle and influence fitness in distant areas and future periods.

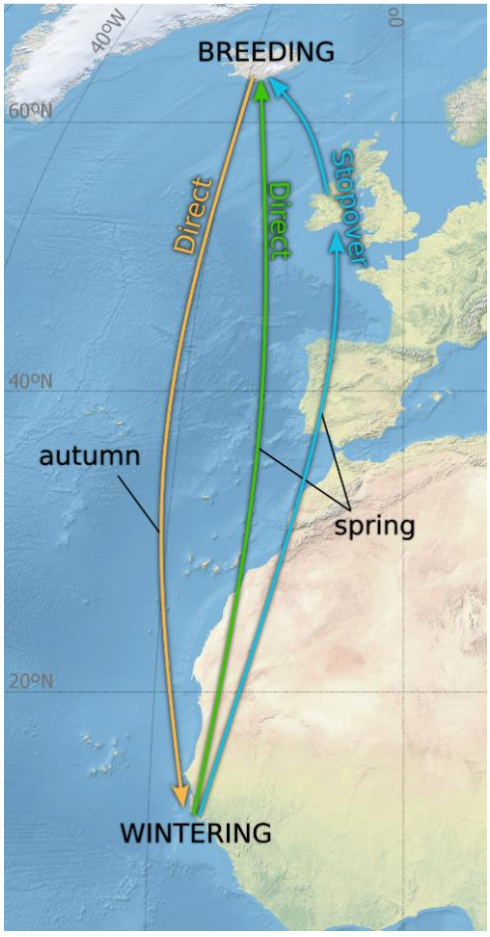
Individual variation

The longevity on several bird species can surpass a decade and long lived individuals tend to be considerably consistent during their lifetime, both in space (e.g. breeding and wintering in the same sites every year) and in time (e.g. migrating approximately on the same date every year; Conklin et al. 2013, Carneiro et al. 2019a). Although timing is important, the costs of being earlier or later than the optimal date can vary and selection for optimal timing of events might not be equally strong between different stages of the annual cycle. For example, due to the importance of timing of breeding (Perrins 1970, Drent 2006, Morrison et al. 2019), selection on timing during the preceding spring migration is expected to be stronger than in autumn (McNamara et al. 1998). Under strong time selection, the available strategies for individuals (e. g. schedules) are likely to be fewer than when selection is more relaxed and individuals can perform a given task (e. g. migration) over a wider time window (Madsen 2001, Warnock et al. 2004). Thus, both consistency and flexibility can be advantageous, depending on the life history of a given species (Vardanis et al. 2016). While individual consistency can differ among distinct annual events (e.g. Conklin et al. 2013, Verhoeven et al. 2019), the performance of individuals at a given stage may also depend on the conditions experienced during previous stages (Harrison et al. 2011, O'Connor et al. 2014). Therefore, consistent behaviour at one stage might limit the degree of change in the subsequent one.

Study system: Icelandic whimbrel

Whimbrels *Numenius phaeopus* are large long-distance migratory waders, with a typical lifespan of 11 years and a longevity record of 24 years (Robinson 2018). Their breeding distribution expands mainly along the sub-arctic and high temperate latitudes (with exceptions: e.g. *N. p. alboaxillaris*), and in the winter they can be found along almost all coastal areas in temperate and tropical regions (van Gils et al. 2019). Whimbrels tend to be faithful to the breeding and wintering sites (Mallory 1982, Zwarts 1990, McNeil and Rompre 1995, BWPi 2006), and perform a complete feather moult in winter (Ginn and Melville 1983). There are seven subspecies recognized (although classification is not settled; van Gils et al. 2019). The Icelandic whimbrel *N. p. islandicus* (Fig. 1.2) breeds almost exclusively in Iceland, but some pairs can also be found in Greenland, the Faroe Islands and northern Scotland (van Gils et al. 2019). In Iceland, the breeding population is estimated to be 256000 pairs (Skarphéðinsson et al. 2016), which encompasses more than 25% of the world population of this species (Delany and Scott 2002). During winter, Icelandic whimbrels can be found along coastal areas from temperate regions in south-west Europe to tropical areas in Benin and Togo, but most

Figure 1.2. Icelandic whimbrel under a warm sunlight, Iceland. Photo by Tómas G. Gunnarsson.



tracked individuals migrate to the Guinea-Bissau/Guinea-Conakry region (Gunnarsson and Guðmundsson 2016, Alves et al. 2016, Carneiro et al. 2019b).

Although it was suspected that Icelandic whimbrels fly directly from Iceland to the wintering sites and that when returning in spring make at least one stopover (Gunnarsson and Guðmundsson 2016), this was only recently confirmed by tracking individuals with geolocators (Alves et al. 2016; see Box 1). By successfully tracking four birds, that study also recorded non-stop flights during spring migration, information that was later extended with the tracking a larger sample of individuals (Carneiro et al. 2019b). It is now well established that while in autumn mainly one migratory

Figure 1.3. Scheme of the main migratory strategies of Icelandic whimbrels. In autumn, most individuals fly directly from the breeding to the wintering areas (in orange); in spring, most perform a flight to a stopover location, usually in Britain and Ireland, and another flight to Iceland (in blue) or fly directly (in green; Alves et al. 2016, Carneiro et al. 2019a, b).

strategy exists, with birds migrating non-stop to the wintering areas, two strategies have been identified in spring (Fig. 1.3): a direct strategy, when individuals perform a single flight; and a stopover strategy, when most individuals perform one flight to a stopover area, usually in Britain and Ireland, and a second flight from there to Iceland (Alves et al. 2016, Carneiro et al. 2019b). The stopover strategy occurred in ca. 80% of the recorded migrations, and individuals have also been recorded changing strategies between years (Carneiro et al. 2019a, b), but only from a direct to a stopover strategy. More recently, a few cases differing from the general pattern were recorded: one individual made a stopover in autumn (Carneiro et al. 2019a) and three made two stops during spring instead of just one (Chapter 5).

Box 1. Geolocators

Geolocators record light intensity at very short intervals (e.g. every 5 minutes) and are mostly used to track animal movements. They have been used for decades, in several animal groups (Delong et al. 1992, Block et al. 1998, Fuller et al. 2008), but only more recently their weight became around 1 g, which allowed its use on many bird species with low body mass (Bridge et al. 2011). Using the pattern of ambient light, the locations for the period that individuals carried the devices can be inferred, because day length and sunrise vary with latitude and longitude. Some of these devices also record temperature, conductivity and wet contacts, which can be used to refine the departure and arrival dates during migration (Battley and Conklin 2017), as these data is recorded at four hour periods and a maximum of two geographical locations per day can be inferred from light data. But applications can go beyond studies on migration. For example, geolocators have been used to study the incubation patterns of waders (Burger et al. 2012, Gosbell et al. 2012) and the activity of seabirds at sea (Jaeger et al. 2017, Ponchon et al. 2019). They are lightweight and cheap, compared to satellite transmitters, but require that the tracked individual is recaptured to remove the device and download the data.

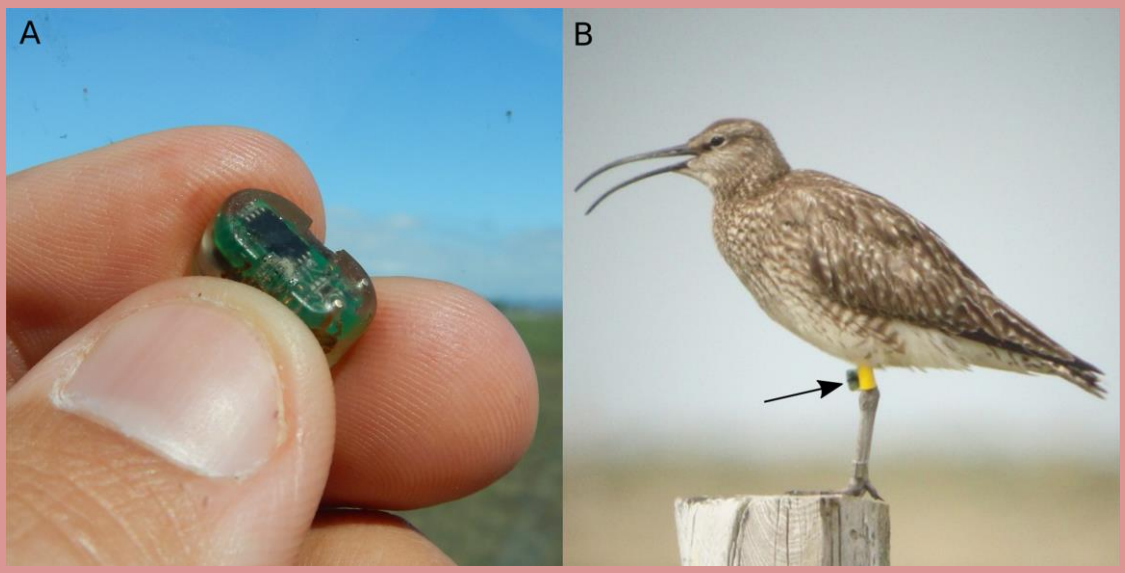


Figure B1.1. (A) Geolocator after retrieval, containing data; model Intigeo-C65 from Migrate Technology Ltd., weighing 1 g. (B) Icelandic whimbrel carrying the same geolocator model attached to a leg flag. Photos by Camilo Carneiro.

Whimbrels arrive into Iceland during late April and the first half of May, and most depart from late July to mid-August (Carneiro et al. 2019b). Their breeding season is one of the shortest among wader species breeding in Iceland (Gunnarsson, unpublished data). They are monogamous and tend to breed with the same partner every year (van Gils et al. 2019). Nests are open, on the ground (Fig. 1.4A), and laying starts in the second half of May, with a peak at the end of that month or in the first days of June (Gunnarsson 2010). Whimbrels lay a single clutch, usually of four eggs, and incubation takes on average 25 days after the last egg is laid and is shared by both adults (van Gils et al. 2019). Upon hatching, whimbrel chicks are precocial and nidifugous, leaving the nest and starting to forage independently within a few hours (Fig. 1.4B). Chicks are reported to fledge at 35-40 days (van Gils et al. 2019), but tend to fly well at ca. 27 days of age (pers. obs.). Both parents provide brood protection during chick development, although females tend to leave the family earlier (BWPi 2006).

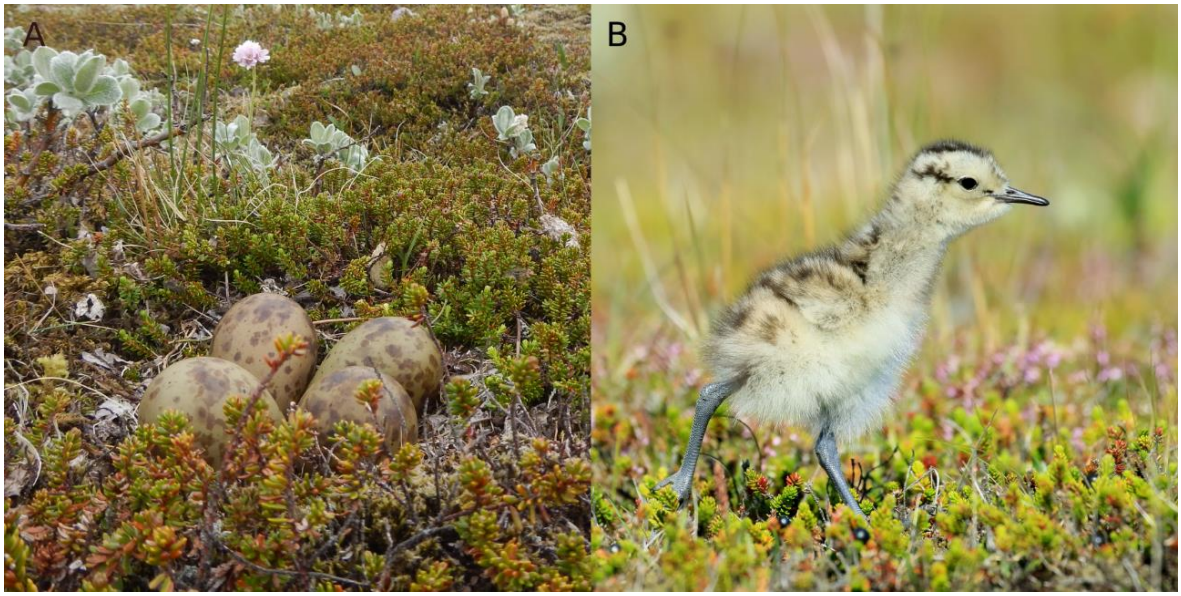


Figure 1.4. (A) Whimbrel nest in Iceland. Clutches tend to be composed by four eggs that are laid in a nest cup on the ground. (B) Whimbrel chick with one to two days of age. Chicks are precocial and nidifugous, leaving the nest and foraging independently (although under adult protection) within a few hours. Crowberries *Empetrum nigrum* also visible in the photos (with ripe fruits on B), which are common in whimbrel nesting habitat in Iceland and both chicks and adults forage on them. Photos by (A) Camilo Carneiro and (B) Tómas G. Gunnarsson.

Background

Climate is changing at a faster pace than some species are able to respond to (Both and Visser, 2001), and this pattern can be more prevalent in the arctic and sub-arctic, where temperatures are increasing more rapidly than at lower latitudes (Høye et al., 2007; Serreze et al., 2009; Cohen et al., 2014). This can be particularly problematic for long-distance migrants, which use different climatic regions during the annual cycle, as the responses to climatic changes at one site (e.g. wintering areas) may influence the possibility to respond later in the annual cycle at another site (e.g. breeding

areas). In fact, long-distance migrants are declining globally and often more so than short-distance migrants and resident species (Sanderson et al. 2006, Morrison et al. 2013).

Several wader species are long-distance migrants and have an unfavourable conservation status (IUCN 2019). Within the Numeniini tribe, which encompasses 13 large-bodied and mostly long-distance migratory waders (eight species of curlew *Numenius spp*., four species of godwit *Limosa spp*. and the Upland Sandpiper *Bartramia longicauda*), only six are of least concern (with caveats; Pearce-Higgins et al. 2017). Whimbrels belong to the latter group, but with populations facing several threats (Brown et al. 2014). In the breeding grounds, Icelandic whimbrels encounter habitat fragmentation due to the expansion of summer cottages and conversion of natural habitats, while in the non-breeding areas habitats are under pressure by direct or indirect human activities (Brown et al. 2014). Nevertheless, the Icelandic population is currently stable (Skarphéðinsson et al. 2016). Furthermore, and intriguingly, while recent research has indicated that most species of waders breeding in Iceland have been advancing their spring arrival dates (e.g. golden plover *Pluvialis apricaria* and black-tailed godwit), accompanying the trend of temperature change, Icelandic whimbrels are not, and show stable spring arrival dates over the last three decades (Gunnarsson and Tómasson 2011, Gill et al. 2014b, Carneiro et al. 2019a).

Most studies have thus far focused on particular periods of the annual cycle, but a full annual cycle perspective is key in order to understand how long-distance migratory birds may respond to the ongoing changes in the environment (Marra et al. 2015).

Objectives

The main aim of this thesis is to understand how different annual strategies influence individual fitness. Variation in annual performance between individuals takes form in migration strategy (direct vs. stopover), phenology of migration, wintering site quality, migration distance and timing of breeding. These topics are investigated in detail in Chapters 2 to 6.

In **Chapter 2**, using 56 migrations from 19 individuals tracked with geolocators over four years, differences in seasonal migration duration, migration speed and ground speed of Icelandic whimbrels are explored, and their migration routes, wintering and stopover areas mapped with this original dataset. In **Chapter 3**, I investigate range wide energetic trade-offs and associated carry-over effects of wintering area conditions into the breeding season. I first calculate the energetic balance achieved at three wintering areas along the population winter range, as established in the previous chapter (Tejo Estuary in Portugal, Banc d'Arguin in Mauritania and the Bijagós Archipelago in Guinea-Bissau). Using flight range models, I estimate the migration flight costs between each wintering area and Iceland, both for a direct and a stopover strategy. I then, test the effect of laying date on fledging success, before investigating carry-over effects of winter condition into breeding performance in the form of timing of laying and breeding investment. **Chapter 4** explores seasonal and sex-specific variation in the consistency of individual timing during the annual cycle, in the light of a population

showing no advancement in spring migration arrival in response to increasing temperatures. In **Chapter 5**, using full annual cycle individual level data, I investigate correlations between annual stages (arrival and departure dates during migration and laying date) and duration of stationary periods (wintering, stopover, arrival-lay gap), and assess their fitness consequences, in the light of extreme long-distance migratory waders. Finally, in **Chapter 6**, I explore how wind conditions, temperature and departure date may influence the spring migratory strategy of Icelandic whimbrels.

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CHAPTER 2

FASTER MIGRATION IN AUTUMN THAN IN SPRING: SEASONAL MIGRATION PATTERNS AND NON-BREEDING DISTRIBUTION OF ICELANDIC WHIMBRELS NUMENIUS PHAEOPUS ISLANDICUS

Camilo Carneiro, Tómas G. Gunnarsson, José A. Alves

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Previous photo by Tómas G. Gunnarsson.
Icelandic whimbrel in flight, Iceland, 23 July 2019.
The average wingspan of Icelandic whimbrels is 87 cm.

FASTER MIGRATION IN AUTUMN THAN IN SPRING: SEASONAL MIGRATION PATTERNS AND NON-BREEDING DISTRIBUTION OF ICELANDIC WHIMBRELS *NUMENIUS PHAEOPUS ISLANDICUS*

Abstract

Migration is fundamental in the life of many birds and entails significant energetic and time investments. Given the importance of arrival time in the breeding area and the relatively short period available to reproduce (particularly at high latitudes), it is expected that birds reduce spring migration duration to a greater extent than autumn migration, assuming that pressure to arrive into the wintering area might be relaxed. This has previously been shown for several avian groups, but recent evidence from four tracked Icelandic Whimbrels (*Numenius phaeopus islandicus*), a long distance migratory wader, suggests that this subspecies tends to migrate faster in autumn than in spring. Here, we (1) investigate differences in seasonal migration duration, migration speed and ground speed of Whimbrels using 56 migrations from 19 individuals tracked with geolocators and (2) map the migration routes, wintering and stopover areas for this population.

Tracking methods only provide temporal information on the migration period between departure and arrival. However, migration starts with the fuelling that takes place ahead of departure. Here we estimate the period of first fuelling using published fuel deposition rates and thus explore migration speed using tracking data. We found that migration duration was shorter in autumn than in spring. Migration speed was higher in autumn, with all individuals undertaking a direct flight to the wintering areas, while in spring most made a stopover. Wind patterns could drive Whimbrels to stop in spring, but be more favourable during autumn migration and allow a direct flight. Additionally, the stopover might allow the appraisal of weather conditions closer to the breeding areas and/or improve body condition in order to arrive at the breeding sites with reserves.

Introduction

Seasonal migration is a fundamental process that occupies a considerable portion of the annual cycle of many birds (Newton 2007) and involves a significant energetic investment (Drent and Piersma 1990). In spring, migration duration might be shorter as arrival dates into the breeding areas are under strong selection. Breeding individuals aim to arrive as early as possible in order to secure a good quality breeding territory and a mate (Kokko 1999) thus increasing the chances of fledging young (McNamara et al. 1998). Additionally, the period of time spent in the breeding areas is particularly relevant as it may increase the number of nesting attempts (Møller 1994). However, early arrival has a limit (Kokko 1999), as unfavourable weather events (e.g. cold spells or snowfall) are frequent early in the season, particularly at high latitudes, and might affect food availability and even cause mortality (Marcström and Mascher 1979). Therefore, birds potentially adjust the pace of

migration to avoid encountering unfavourable conditions upon arrival at the breeding site (Senner et al. 2015). Arrival time can also vary between sexes (e.g. Alves et al. 2012), as the male role in settling and defending a breeding territory can lead to different pressures on the sexes with males arriving before females (Currie et al. 2008). On the other hand, females are also likely to be under pressure not to arrive much later than males in order to avoid divorce or obtain a mate (Gunnarsson et al. 2004, Kokko et al. 2006). After the breeding season, the pace of migration could be slower if the pressure on arrival order is weaker or absent and/or resource and weather conditions are expected to be favourable upon arrival at the wintering areas. In fact, across and within avian groups, migration tends to be faster during spring than autumn (Nilsson et al. 2013, Zhao et al. 2017).

The Icelandic Whimbrel (*Numenius phaeopus islandicus*) is a large, long distance migratory wader that mostly breeds in Iceland and winters in West Africa. Non-stop flights from Iceland to West Africa were suggested by ringing data, but at least some individuals stopover in Ireland, Britain, Belgium or France during spring migration (Gunnarsson and Guðmundsson 2016). However, migration duration was not assessed. Using geolocators, Alves et al. (2016) tracked four birds (two males and two females) and found that all individuals flew directly to West Africa during autumn migration, but during spring two individuals made a stopover in Ireland and Britain, while the remaining two flew non-stop to Iceland. Contrary to the overall trend in birds (Nilsson et al. 2013, Zhao et al. 2017), Alves et al. (2016) results suggested that Icelandic Whimbrels tend to migrate faster in autumn than in spring, despite the first fuelling period being unknown. Is this pattern a result of the small sample size or do Icelandic Whimbrels deviate from the rule of faster spring migrations? Using a larger dataset of Icelandic Whimbrels tracked with geolocators we (1) investigate differences in migration duration, migration speed and ground speed between seasons and sexes and (2) map the migration routes, wintering and stopover areas for this population.

Methods

Whimbrel tracking

Between 2012 and 2015, 40 adult Icelandic Whimbrels were caught on the nest, in the southern lowlands of Iceland (63.8°N; 20.2°W), using a nest trap (Moudry TR60; www.moudry.cz). They were fitted with colour rings and a geolocator attached to a flag on the tibia (n=10 in 2012 and 2014; n=3 in 2013; n=30 in 2015). We used the Intigeo-W65A9RJ model from 2012 to 2014 and Intigeo-C65 in 2015 (Migrate Technology Ltd). In order to retrieve the devices, we recaptured the birds one or more years later using the same technique. A total of 28 geolocators, from 19 individuals (of which five were tracked for more than one year) were retrieved (25 in the following breeding season, plus three two breeding seasons later). Devices retrieved two seasons later recorded two autumn migrations and two wintering periods. One device stopped logging in mid-winter and another shortly after departure from Iceland. In total, we collected information on 30 autumn and 26 spring migrations and corresponding wintering and stopover areas. In 2016, six birds carrying a geolocator deployed in

2015 were recorded on the breeding territories but not recaptured. The overall return rate for Whimbrels carrying geolocators was 64%, which is the same as individuals marked with colour-rings (64%; Katrínardóttir et al. 2015). Ten individuals were sexed using biometrics following Katrínardóttir et al. (2013), three molecularly (as in Katrínardóttir et al. 2013) and six through behavioural observation (copulating position or scraping of a nest cup which is only performed by males).

Geolocator data analysis

Data were downloaded using IntigeoIF and light data were analysed with IntiProc (both Migrate Technology Ltd) and R package '*Geolight'* (Lisovski and Hahn 2012). A threshold of 3 was used to define twilight events. After preliminary steps to visually check for errors in twilight events and calibration (see Appendix 2.1 for details), geographical positions were generated (sun elevation angle ranged from -6 to -4.7), filtered (k=2, on *loessFilter* function of '*Geolight'*) and double smoothed. Both equinoxes occur during the wintering period, and given that Whimbrels display territorial behaviour during the winter season (Mallory 1982, Zwarts 1990), we assumed they remain on the same area and thus a 40 day period centred on each equinox was excluded from subsequent analysis.

Geolocator light data allows estimating a maximum of two positions per day, one by midday and another by midnight. However, temperature was measured every five minutes with minimum and maximum values stored every four hours, and conductivity and wet/dry sampled every 30 seconds with maximum conductivity and amount of wet contacts stored every four hours (Mode 1 was used; see manufacturer info for more details). These 4h intervals provide a finer temporal resolution of the timing of events (e.g. departure and arrival) than the 12h intervals between locations derived from light data (Battley and Conklin 2017) and were used to determine timing of events to within four hours (see Appendix 2.1 for details).

Defining migratory tracks, duration, speeds and wintering and stopover areas

We assumed the last/first geographical position on land to be the one temporally closest to the time defined by the temperature, conductivity and wet contacts and the first/last position in flight the one immediately after/before the one on land. We assumed the starting point of autumn migration to be in the Icelandic breeding area (63.8°N; 20.2°W) and its end in the first position on land when reaching the wintering area (with one exception; see Appendix 2.1). Similarly, spring migration was considered to start in the mean wintering position (average location of all points recorded during the period spent in Africa; with five exceptions; see Appendix 2.1) and ending in the first position on land when reaching Iceland. The first and last position at the stopover site (which usually are not the same due to geolocation accuracy or bird movement) were linked with a linear segment and its distance was considered for migration speed and distance but not for ground speed estimation. The distance between positions was calculated as the great circle distance using the function *distCosine* of the R package '*geosphere'* (Hijmans 2016).

Migration effectively starts with the fuelling period prior to the first migratory flight (Alerstam and Lindström 1990). We estimated this period by calculating how long Whimbrels take to store the required fuel to cover the first flight. Flight 1.25 (Pennycuick 2008) was used to build a flight model to estimate how much fuel, as percentage of lean body mass (LBM), is necessary to cover the distance of the first recorded flight (see Appendix 2.2). The required fuel load (% of LBM) was then divided by a fuel deposition rate (FDR) at 1.78% of LBM/day, which is the population maximum reported for Whimbrel (Lindström 2003). The resulting period (in days) was added to the travel duration (i.e. to the period recorded between first flight departure and arrival at final destination), resulting in migration duration.

Migration speed was calculated as the ground distance travelled divided by migration duration. To estimate ground speed during migration, we calculated the speed between consecutive positions during migratory flights, considering only the positions between the last on land and the last in flight. Three very high speeds of 34.5, 37.8 and 41.8ms^{-1} were checked for the possibility of being outliers. However, as the speed during the preceding and following segments were within range of recorded values (i.e. not abnormally low), these were included in the analysis. Excluding these values does not change the results (see Appendix 2.3).

The wintering and stopover areas were estimated by calculating the kernel densities encompassing 50%, 75% and 95% of the locations generated on each period by all birds, using the R package '*adehabitatHR*' (Calenge 2006) with a smoothing parameter computed by least-squares cross validation.

Statistical analysis

In order to test seasonal (autumn vs. spring) differences in migration duration, migration speed and ground speed of Icelandic Whimbrels, linear mixed models (LMM) were used with season, sex and their interaction as fixed effects, and individual as a random effect. Function *lmer* in R with restricted maximum likelihood (package '*lme4*'; Bates et al. 2015) was used and statistical significance of fixed effects was calculated with package '*lmerTest*' (Kuznetsova et al. 2016).

Results

The mean (±SE) total migration distance for Icelandic Whimbrels was 6079 ± 68km in autumn and 6450 ± 118km in spring (Table 2.1). Winter kernel densities indicate that the wintering area of this population encompasses Sierra Leone, Guinea-Conakry, Guinea-Bissau, Senegal, The Gambia, Mauritania and Morocco, with the highest density of the locations in Guinea-Conakry and Guinea-Bissau (Figure 2.1). On spring migration, the stopover areas used were Ireland, western Britain, NW France and Portugal (Figure 2.1C and 2.1D) with the highest concentrations in Ireland.

On average, males departed later than females on autumn migration (although the difference is not statistically significant: Mann-Whitney-Wilcoxon test W=77, p=0.18; Table 2.1), possibly because males attend the broods longer than females (BWPi 2006). All birds flew directly from Iceland to the wintering sites (n=30 autumn migrations from 19 individuals; Figure 2.1A and 2.1B). Males departed earlier than females in spring (Table 2.1) and made a stopover in 83% (n=18) of the cases, while females stopped in 75% (n=8) of the occasions (data from 19 individuals; Figure 2.1C and 2.1D). Males arrived into Iceland on average 2 days before females (males: 7 May ± 5 days; females: 9 May ± 6 days), but the difference is not statistically significant (Mann-Whitney-Wilcoxon test W=89, p=0.37).

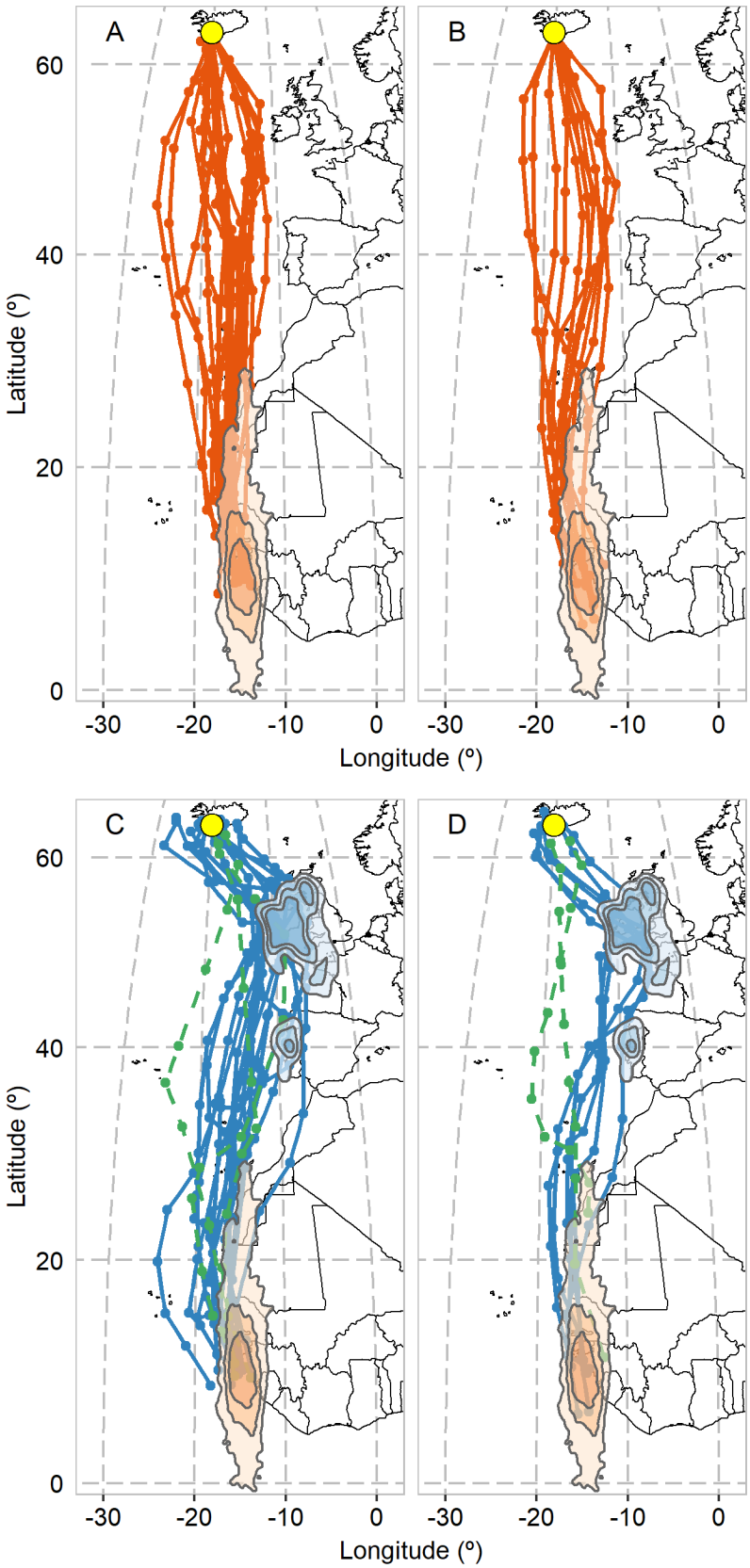

Figure 2.1. Icelandic Whimbrel migration routes as tracked by geolocators, between 2012 and 2016, in autumn (A–B) and spring (C–D), displayed separately for each sex (male: A and C; females: B and D). Polygons represent kernel densities of 95, 75 and 50%, from pale to dark, respectively, for winter (orange) and stopover areas (blue). The yellow circle represents breeding site.

Table 2.1. Seasonal migration parameters for male and female Icelandic whimbrel, tracked between 2012 and 2016.

	Autumn										Spring									
	Males					Females					Males					Females				
	n	mean	sd	min	max	n	mean	sd	min	max	n	mean	sd	min	max	n	mean	sd	min	max
Departure date (days)	20	12-Aug	5.7	3-Aug	21-Aug	11	7-Aug	8.3	25-Jul	17-Aug	18	22-Apr	2.9	16-Apr	27-Apr	8	23-Apr	4.0	18-Apr	29-Apr
Arrival date (days)	19	16-Aug	5.9	7-Aug	26-Aug	11	11-Aug	8.6	28-Jul	21-Aug	18	7-May	5.1	25-Apr	11-May	8	9-May	5.6	29-Apr	14-May
Total duration (days)	19	59.2	1.7	53.7	62.2	11	59.2	3.9	47.9	62.4	18	62.4	5.3	52.2	73.9	8	62.5	8.3	48.7	73.5
Estimated fuelling period for the first flight (days)	19	54.8	1.6	48.9	56.2	11	55.2	3.7	44.4	57.9	18	50.2	5.0	37.4	58.3	8	49.5	2.8	44.1	52.5
Stopover duration (days)											15	11.4	3.0	6.5	17.2	6	14	2.1	10.8	16
Total migration distance (km)	19	6053	242.8	5180	6264	11	6125	540.3	4585	6552	18	6496	443.1	5195	7251	8	6346	888.7	4534	7327
Total migration speed (kmd^{-1})	19	102.0	1.7	96.5	103.9	11	103.0	2.9	95.6	106.1	18	99.0	4.9	93.0	108.6	8	96.8	6.2	88.9	105.2
Ground speed (ms^{-1})	150	16.00	6.19	0.69	41.76	80	17.46	5.51	5.87	37.83	169	12.85	6.04	1.57	32.36	72	13.58	5.26	2.89	26.87

Table 2.2. Model results testing differences in migration duration (A), migration speed (B) and ground speed (C) of Icelandic whimbrels between seasons and sexes; estimates for sex are of male in relation to female, for season is of spring in relation to autumn.

		Fixed effects						Random effects		
	n		Estimate	SE	df	*t*	*p*		Variance	SD
(A) Migration duration	56	Intercept	57.69	1.95	19.75	29.61	**<0.001**	individual	15.96	4.00
		season	7.02	1.52	34.23	4.63	**<0.001**	Residual	10.48	3.24
		sex	1.42	2.37	20.41	0.60	0.555			
		season*sex	-0.80	1.86	34.18	-0.43	0.671			
(B) Migration speed	56	Intercept	102.79	1.35	24.62	76.23	**<0.001**	individual	3.29	1.81
		season	-6.31	1.66	36.78	-3.81	**<0.001**	Residual	12.61	3.55
		sex	-0.60	1.67	27.04	-0.36	0.720			
		season*sex	3.56	2.03	36.59	1.76	0.087			
(C) Ground speed	472	Intercept	17.25	0.75	30.13	22.93	**<0.001**	individual	0.62	0.79
		season	-3.77	0.96	465.22	-3.93	**<0.001**	Residual	34.49	5.87
		sex	-1.28	0.92	33.35	-1.38	0.176			
		season*sex	0.52	1.16	463.78	0.45	0.656			

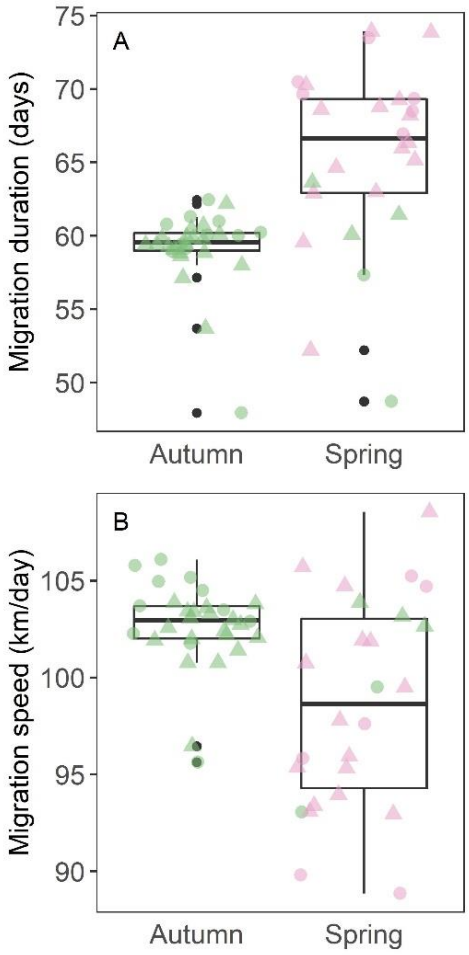

Figure 2.2. Autumn and spring migration duration (A) and migration speed (B) of Icelandic Whimbrels; boxes show the median and 25 and 75% quartiles, whiskers extend up to 1.5 times the inter quartile range from the hinge and points beyond that are individually marked in black; all data points overlay the boxplots, coloured by strategy (green: direct; pink: stopover) and sex (dots: females; triangles: males).

Migration duration was significantly different between seasons, being 59.2 ± 2.6 days in autumn and 65.5 ± 6.2 in spring, with no apparent differences between sexes within season (Tables 2.1 and 2.2A; Figure 2.2A). Likewise, migration speed and ground speed were higher in autumn than in spring (migration speed: 102.6 ± 2.2 kmd^{-1} in autumn and 98.6 ± 5.3 kmd^{-1} in spring; ground speed: 16.50 ± 5.99 ms^{-1} in autumn and 13.07± 5.82 ms^{-1} in spring), with no differences between sexes (Tables 2.1, 2.2B and 2.2C; Figure 2B).

Discussion

Icelandic Whimbrels' migration speeds are within the range for flapping migrants (26 to 175-200 kmd^{-1}, Hedenstrom and Alerstam 1998). During autumn migration, when compared to waders migrating through Scandinavia, their speed is relatively high (102.6 kmd^{-1} vs. ca. 40-115 kmd^{-1}, Alerstam and Lindström 1990) and higher than in spring (Table 2.1 and 2.2B). Migrating faster during autumn, is probably counterintuitive given the time pressure for early arrival in spring (Møller 1994, McNamara et al. 1998, Kokko 1999). But migration duration and speed do not necessarily indicate time constraints or individual migratory strategies, as environmental conditions can differ markedly between seasons. Nevertheless, faster autumn migrations are unusual among migratory birds (Nilsson et al. 2013, Zhao et al. 2017) and several factors may contribute to such a seasonal difference in Icelandic Whimbrels.

All tracked birds undertook a direct flight to the winter areas in autumn, while in spring most made a stopover (Table 2.1). External factors such as wind conditions, can differ between seasons (Kemp et al. 2010) and contribute to the stopover during spring. For example, despite preparing for a direct flight from wintering areas in Mauritania to a major stopover in the Wadden Sea (North Europe), Red Knots (*Calidris canutus canu*tus) make an additional stopover in West France when wind conditions are unfavourable (Shamoun-Baranes et al. 2010). This might also be the case for Whimbrels, as unfavourable wind conditions are more prevalent during spring than autumn migration (Alves et al. 2016), and the recorded ground speed was lower in spring (Table 2.1).

The main stopover area used by Icelandic Whimbrels, Ireland, is ca. 1500 km from the breeding areas (Figure 2.1). A cross-species comparison shows that species wintering closer to Iceland generally show a stronger correlation between timing of arrival and weather conditions in Iceland, than species wintering further away (Gunnarsson and Tómasson 2011). This suggests that Whimbrels' stopover closer to Iceland may facilitate tuning of arrival on the breeding grounds. Alternatively, Icelandic Whimbrels could appraise conditions on flight and dynamically adapt the migratory strategy accordingly. If conditions are expected to be unfavourable at the breeding areas, then making a stopover might be the best option as arriving too early may increase the risk of mortality due to stochastic weather events (Marcström and Mascher 1979). This mechanism was described for the Black-tailed Godwit (*L. limosa islandica;* Alves et al. 2012), another Icelandic breeding wader, which although migrating shorter distances, individuals wintering in Iberia move first to an area closer to Iceland (e.g. Britain or the Netherlands), likely to be able to appraise conditions in the breeding areas (Gunnarsson and Tómasson 2011, Alves et al. 2012).

Furthermore, Whimbrels might be unable to routinely migrate fast in spring if they cannot (or only rarely) accumulate enough energy for a direct flight from the wintering to the breeding areas. At one important wintering site in West Africa, the Banc d'Arguin, it was shown that prey availability (crabs, mainly Fiddler *Uca tangeri*) and a digestive bottleneck, constrain resource accumulation by Whimbrels, preventing earlier departure (Zwarts 1990, Zwarts and Dirksen 1990). Such bottlenecks

may also limit Whimbrels in accumulating enough fuel for a direct flight to Iceland. However, it was recently described that Whimbrels wintering in the Banc d'Arguin consume West African Bloody Cockles (*Senilia senilis*), a prey that became available in recent decades (Carneiro et al. 2017) and might allow them to overcome such limitations.

Even if enough fuel is acquired prior to departure and wind support *en route* is favourable, Whimbrels' longer spring migration might occur to improve body condition at arrival (Alerstam 2006). If conditions at stopover allow for a higher rate of resource accumulation than at the breeding areas, individuals that stopover might gain an advantage, despite later arrival, by being in better physiological condition than individuals that flew directly (Alerstam 2006). Such overload of resources has been described for other waders and might allow time saving in the breeding sites by starting energy-demanding activities (e.g. display flights) as quickly as possible (Davidson and Evans 1988, Gudmundsson et al. 1991). In fact, tracked Whimbrels have been observed in the breeding territories on the same or within a few days of arrival into Iceland, sometimes engaging in territorial disputes (pers. obs.).

Although several waders are income breeders (Klaassen et al. 2001), some species are known to use resources from stopover areas to produce eggs (Hobson and Jehl 2010). Female Hudsonian Whimbrels (*N. p. hudsonicus*), for which evidence suggests the transport of capital for egg production (Hobson and Jehl 2010), have a similar spring migration strategy to Icelandic Whimbrels (i.e. long flights and one stopover; Johnson et al. 2016). But the stopover duration and migration timings between these populations are different, with the Icelandic Whimbrel spending, on average, shorter periods on spring stopover (ca. 12 days versus ca. 34) and a longer period in Iceland between arrival and laying (ca. 22 days, n=26, versus ca. 11; Hobson and Jehl 2010, Johnson et al. 2016). Hence, Icelandic Whimbrels are less likely to accumulate reserves for egg production during their shorter stopover, and stopover is certainly not compulsory, as direct flights from the wintering areas to Iceland were observed in both sexes. However, capital breeding cannot be excluded across the population given the observed range of stopover duration (Table 2.1) and between arrival and laying (14-31 days for females, n=8; 12-37 days for males, n=18).

During autumn migration all Whimbrels flew directly from Iceland to the wintering area (Figure 2.1). Non-stop flights over water could be the most economic option in terms of time and energy and/or provide a route likely free of predators, parasites and pathogens, as proposed for Bar-tailed Godwits (*L. lapponica baueri*, Gill et al. 2009). These flights could be more common in autumn than spring if wind patterns are more favourable in that season. In fact, Alves et al. (2016) found Whimbrels experienced more wind support during autumn than spring migration. An alternative explanation for a shorter duration of migration in autumn is that arrival order into the wintering areas is relevant, with earlier birds acquiring/maintaining the best quality territories (Zwarts 1990). Additionally, by arriving early, the available time to perform the annual complete moult could be maximized, but such time constraints might not occur even if individuals are very late, as moult ends in November/January (Ginn and Melville 1983) and spring migration fuelling does not start until March (Table 2.1).

Migration starts with the first fuelling period (Alerstam and Lindström 1990), which is very hard to measure and often neglected. To overcome this limitation and calculate migration duration, we estimated how long individuals likely require to store enough fuel for the first flight using a published FDR for Whimbrels (Lindström 2003). Our comparisons could be affected by assuming the same FDR across seasons and areas. Indeed, considering a lower or higher FDR, of 1% or 3%, the statistical differences on migration duration and speed disappear at a FDR of 1% (102.0±4.6 and 104.5±8.1 days of migration duration and 59.5±1.2 and 61.8±3.7 kmd^{-1} of migration speed in autumn and spring, respectively; Appendix 2.3, Table A2.3.2), but not at a FDR of 3% (36.9±1.6 and 45.1±5.8 days of migration duration and 164.9±4.2 and 143.9±11.9 kmd^{-1} of migration speed in autumn and spring, respectively; Appendix 2.3, Table A2.3.3). Despite this limitation, and whilst acknowledging the difficulty of recording the first fuelling period of migration, this approach allows estimating migration duration and speed using tracking data.

Overall, the most parsimonious explanation for the migration patterns described here may combine the external effects of wind and the constraints at the destination. While in autumn winds are likely more favourable and environmental conditions in the wintering areas at arrival more predictable, in spring, unfavourable winds, unpredictable environmental conditions in Iceland and the need to arrive in good physiological condition might result in lower migration speeds. A detailed analysis of wind effects on migratory flights and of individual body condition at arrival in Iceland and/or during stopover should improve our understanding of such seasonal difference in migration speed.

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Appendices

Appendix 2.1

1. *Preliminary steps to check for errors in twilight events and calibration*

We performed a preliminary step using a provisional sun elevation angle (SEA) of -6 to generate geographical positions and visually define provisional last and first positions on land (i.e. before and after migratory flight). Then, we manually checked for errors on twilight events during migratory periods and corrected them when necessary (Figure A2.1.1). To calculate the final SEA, we ran the *loessFilter* function (k=2) and used the Hill-Ekstrom calibration (Lisovski et al. 2012) for the period from 3 days after arrival to wintering areas (usually on first half of August) until 23 November (i.e. ~2 months after autumn equinox). SEAs ranged from -6 to -4.7.

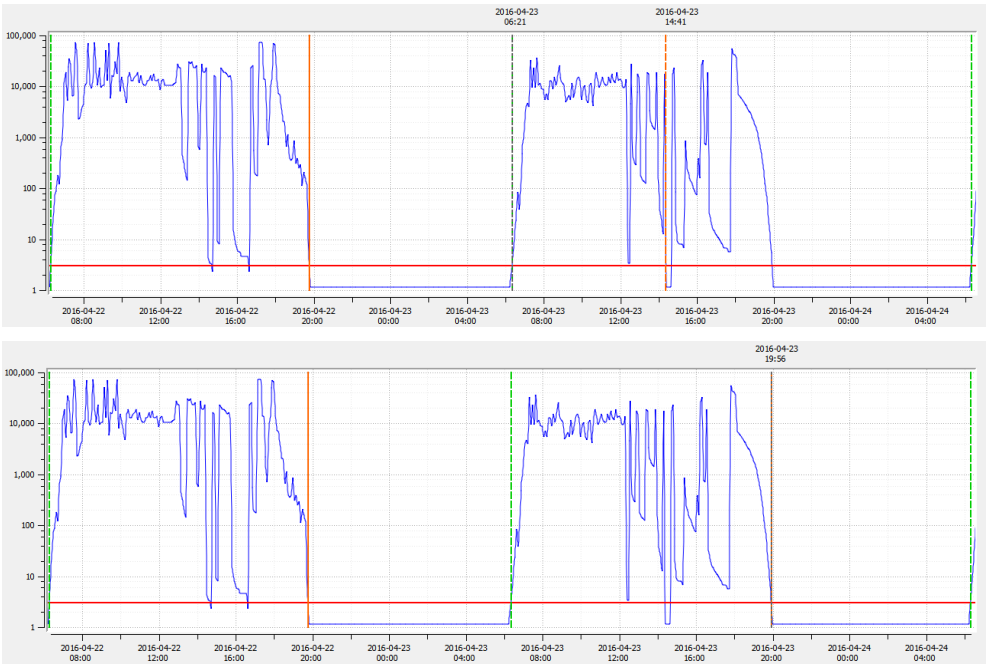

Figure A2.1.1. Example of visual adjustment of twilight events during migratory periods; in this case, on 23 April 2016 an incorrect sunset was defined at 14:41 (top) and was moved to 19:56 (bottom).

2. *Determining timing of events through conductivity, wet contacts and temperature*

We expected temperature to be different at both ends of the migration of Icelandic Whimbrels (Iceland and West Africa) and that behaviour would also differ, with the use of saline water and tidal habitats in West Africa but not on the breeding grounds in Iceland. Assuming that during migration (a) conductivity and (b) wet contacts are likely to be zero, as no water is touching the device pins (albeit dirt such as mud might cause conductivity and/or wet readings), (c) thermal amplitude (tmax-tmin) is likely to be low because the bird is in a relatively homogenous environment and performing the same behaviour and that (d) the overall pattern of variation on these parameters are likely to be distinct when in migratory flight or not, we visually inspected the profiles of minimum temperature, thermal amplitude, conductivity and wet contacts in a window of 48h around the *tFirst* time (i.e. the early twilight time that define the position; Figure A2.1.2) of the last and first positions on land (start

and end of migration, respectively). In these periods we searched for one or more of the following: (a) sudden change (drop or increase) in conductivity, (b) in wet contacts, (c) in thermal amplitude and/or (d) in minimum temperature; the change in the overall pattern of these parameters before departure and after arrival was then used to define the departure and arrival timings (Figure A2.1.2).

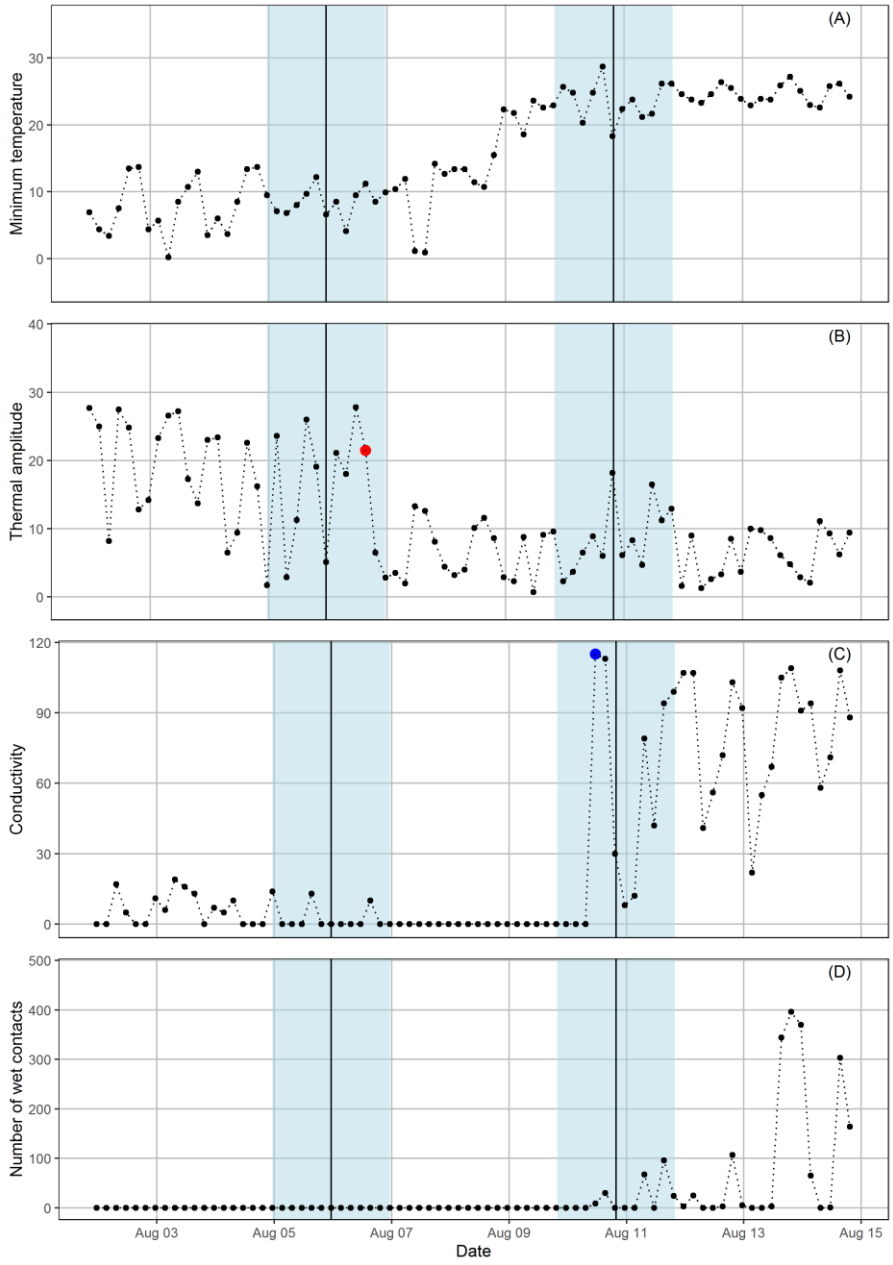

Figure A2.1.2. Example of timings fine-tuning through conductivity, wets and temperature data. Black vertical lines represent *tFirst* (time of last and first geographical positions on land) and the shaded light blue areas a 48h window around it, where departure and arrival timings were searched for based on (A) minimum temperature, (B) thermal amplitude, (C) conductivity and (D) wet contacts. Red and blue circles represent the time assumed for the last (departure) and first (arrival) positions on autumn migration, respectively.

3. Details on defining migratory tracks and speeds

On the winter quarters, the first and last positions on land, i.e. at the end of autumn migration and start of spring migration respectively, did not always coincide with the overall mean wintering position (average location of all points recorded during the period spent in Africa; also referred as 'winter location' henceforward). This was expected due to geolocation precision (ca. 200km; Phillips et al. 2004, Shaffer et al. 2005, Fudickar et al. 2012) and Whimbrel's behaviour (e.g. spending high tide within mangroves, sitting or roosting with the leg with geolocator tucked in the body feathers, causing shading and potentially affecting sunrise and sunset estimate). Such differences were on average 329±192km (range 40-683; n=29) for autumn (excluding geolocator U190, see below) and 385±238km (range 81-1064; n=26) for spring. All these discrepancies were analysed to investigate the possibility of a small staging event before completion of autumn migration. When there was no evidence (by checking temperature, conductivity and wet profiles) of a stationary period on these discrepancies we considered that this position represented arrival to winter location and therefore assumed that autumn migration had been completed. Departure location for spring migration was defined the as winter location but on five cases initial movement southwards was observed at spring departure. We considered this was unlikely and due to geolocation precision errors through shading and assumed migration from the first position on the track northwards. The final part of autumn migration recorded by geolocator U190 indicated a very fast flight up to the equator followed by a return movement to the wintering location (coast of Guinea). We assumed such movement to be a measurement error and excluded it from speed and distance calculations, thus considering migration only up to the first position closer to the winter location.

Appendix 2.2

1. Flight model

In order to calculate migration costs, data on wingspan, wing area, body mass prior to migration, fat fraction and muscle fraction are required. All these were recorded from Whimbrels in Iceland (Table A2.2.1). The sex of each individual was determined through behavioural observations (2 individuals), following Katrínardóttir et al. (2013) equation (15 individuals) and the molecular procedure described therein (4 individuals, plus 6 whose partner was molecularly sexed). For each individual, the wingspan was measured to the nearest mm with a tape measure, the right wing traced and the area calculated following Pennycuick (2008). Muscle fraction was measured from two dead individuals found fresh in Iceland. Fat fraction was estimated as the fraction lost by the heaviest individual in the population flying in the model until reaching the body mass of the lightest (i.e. with no fuel reserves, Pennycuick 2008). The body mass of the heaviest bird was measured just prior departure from Iceland, on 17 August and the lightest upon arrival, on 8 May. Models were produced in Flight (ver. 1.25, Pennycuick 2008) with default parameters described by Pennycuick and Battley (2003), except air density that at start was at 0m and cruising altitude was set for 1500m.

Table A2.2.1. Parameters of Icelandic Whimbrels used in Flight 1.25 to estimate flight costs during migration.

	Females	n	Males	n
Wingspan (m)	0.877	14	0.861	13
Wing area (m^2)	0.088	14	0.083	13
Body mass (kg)	0.601	1	0.601	1
Fat fraction	0.371	-	0.371	-
Muscle fraction	0.18	2	0.18	2
Cruising altitude	1500	-	1500	-

Appendix 2.3

1. *Ground speed comparison between seasons and sex, excluding extreme high values*

Table A2.3.1. Model results testing differences in ground speed of Icelandic Whimbrels between seasons and sexes, excluding three high values of speed (34.5, 37.8 and 41.8ms^{-1}; n = 469); estimates for sex are of male in relation to female, for season is of spring in relation to autumn and for stopover duration is the expected in relation to recorded duration.

		Fixed effects						Random effects		
	n		Estimate	SE	df	*t*	*p*		Variance	SD
Ground speed	469	Intercept	16.75	0.74	33.46	22.77	**<0.001**	individual	0.62	0.79
		season	-3.28	0.93	462.32	-3.54	**<0.001**	Residual	31.72	5.63
		sex	-0.97	0.90	36.57	-1.07	0.290			
		season*sex	0.20	1.12	461.03	0.18	0.860			

2. *Seasonal and sex differences in migration duration and speed, considering fuel deposition rates of 1% and 3%*

Table A2.3.2. Model results testing differences in (A) migration duration and (B) migration speed between seasons and sexes, considering a fuel deposition rate of 1% of lean body mass; estimates for sex are of male in relation to female, for season is of spring in relation to autumn and for stopover duration is the expected in relation to recorded duration.

		Fixed effects						Random effects		
	n		Estimate	SE	df	*t*	*p*		Variance	SD
(A) Migration duration	56	Intercept	99.81	2.84	18.92	35.10	**<0.001**	individual	39.38	6.28
		season	3.00	1.75	34.65	1.71	0.096	Residual	13.92	3.73
		sex	1.42	3.45	19.29	0.41	0.687			
		season*sex	-0.36	2.14	34.63	-0.17	0.867			
(B) Migration speed	56	Intercept	59.25	0.96	23.82	61.48	**<0.001**	individual	2.61	1.62
		season	1.13	1.02	36.10	1.11	0.274	Residual	4.73	2.17
		sex	0.34	1.18	25.39	0.29	0.777			
		season*sex	1.74	1.24	35.99	1.40	0.171			

Table A2.3.3. Model results testing differences in (A) migration duration and (B) migration speed between seasons and sexes, considering a fuel deposition rate of 3% of lean body mass; estimates for sex are of male in relation to female, for season is of spring in relation to autumn and for stopover duration is the expected in relation to recorded duration.

		Fixed effects						Random effects		
	n		Estimate	SE	df	*t*	*p*		Variance	SD
(A) Migration duration	56	Intercept	35.84	1.57	20.63	22.89	**<0.001**	individual	7.31	2.70
		season	9.07	1.61	33.34	5.65	**<0.001**	Residual	11.75	3.43
		sex	1.25	1.92	22.03	0.65	0.522			
		season*sex	-0.96	1.96	33.24	-0.49	0.628			
(B) Migration speed	56	Intercept	166.21	2.68	25.81	62.00	**<0.001**	individual	2.68	1.64
		season	-25.36	3.96	40.68	-6.41	**<0.001**	Residual	72.26	8.50
		sex	-2.39	3.36	29.25	-0.71	0.481			
		season*sex	6.57	4.84	40.34	1.36	0.183			

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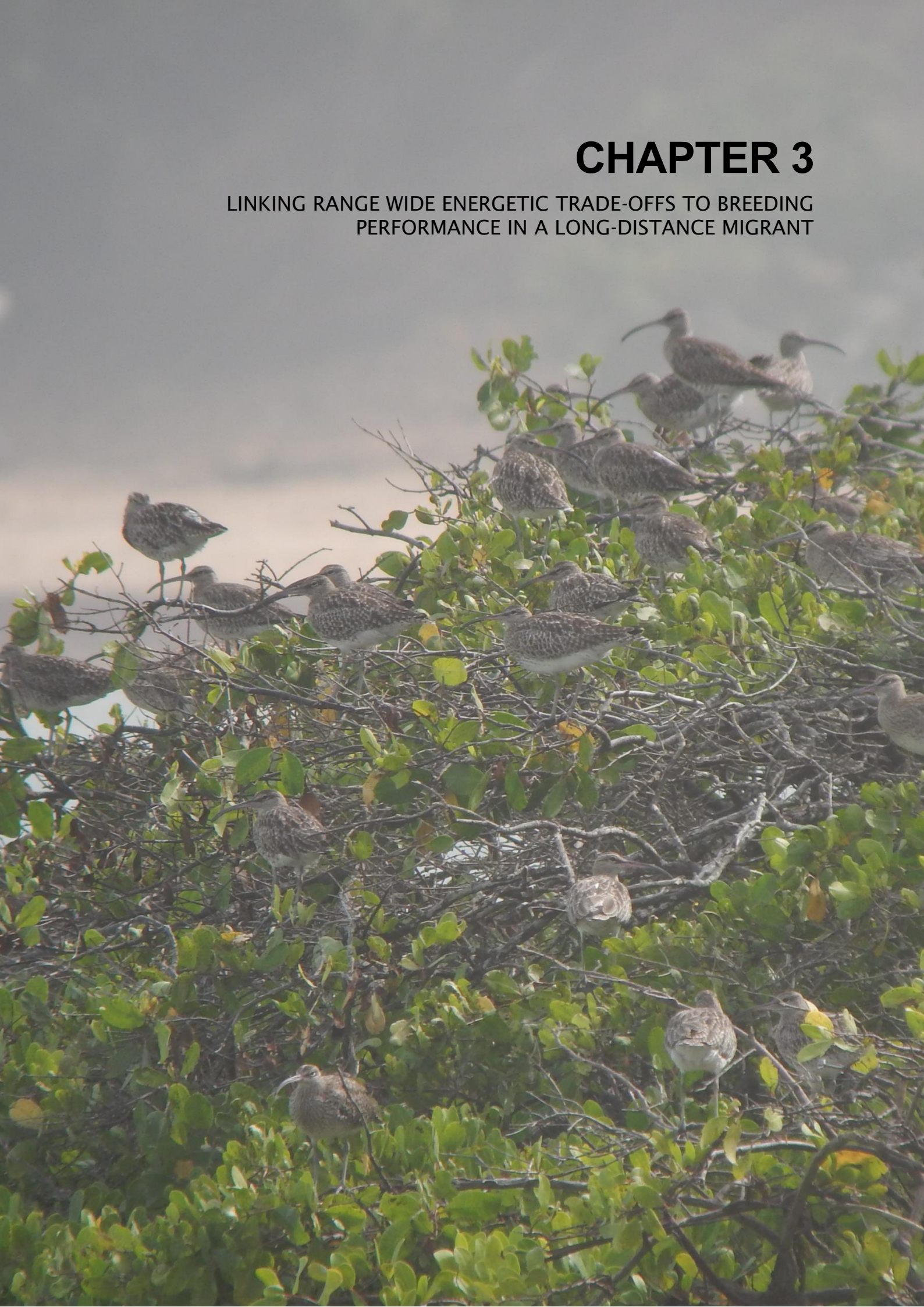
CHAPTER 3

LINKING RANGE WIDE ENERGETIC TRADE-OFFS TO BREEDING PERFORMANCE IN A LONG-DISTANCE MIGRANT



Previous photo by Camilo Carneiro.
Whimbrels on a mangrove, Guinea-Bissau, 27 January 2016.
During high tide, in the Bijagós Archipelago, most whimbrels roost on the abundant mangroves.

LINKING RANGE WIDE ENERGETIC TRADE-OFFS TO BREEDING PERFORMANCE IN A LONG-DISTANCE MIGRANT

Abstract

Understanding how trade-offs and carry-over effects along the annual cycle influence individual fitness is fundamental to unravel variation on population dynamics. However, such data is particularly challenging to collect in long-distance migrants and most studies tend to focus on singular parts of the annual cycle (e.g. breeding). Here, using a full annual cycle approach we investigate Icelandic whimbrel's trade-offs across its entire distribution range, linking breeding parameters (laying date and egg volume) and migration costs to wintering energetic balance experienced throughout the range (from temperate regions in SW Europe to tropical areas in the Gulf of Guinea).

We found that Icelandic whimbrels traded-off higher costs of migration with more favourable wintering conditions, in terms of energetic balance. By migrating further, individuals experienced lower thermoregulatory costs and higher net energetic intake rates, resulting in a more positive energetic balance during the winter. However, these differences did not appear to carry-over into the breeding season in terms of measurable effects on laying date (and, consequently, fledging success) or egg volume, suggesting that individual fitness is unlikely to be significantly influenced by wintering conditions. Nevertheless, Icelandic whimbrels seem to favour wintering locations where the energetic balance is more positive, as the abundance of individuals at the wintering sites reflects the variation in energetic balance.

Introduction

The distribution of many migratory species extends across wide regions of the globe and varies seasonally, through individual migrations between breeding and non-breeding areas (Chapman et al. 2014, Somveille et al. 2018). Within a breeding population, individuals can vary in life-history decisions for example where to migrate for the winter season, which may determine their fitness and can ultimately scale up to influence population dynamics (Norris 2005). To understand how these processes operate and vary across a population, both life-history trade-offs and an annual cycle perspective on the relationships between distinct stages must be established at the individual level (Marra et al. 2015).

Trade-offs are ubiquitous in nature, with individuals allocating time or energy to a given activity at the expense of another, balancing conflicting requirements in order to maximise their fitness. Migration can be costly in terms of energy, time and predation risk (Alerstam and Lindström 1990) and within the same population individuals can vary considerably in migratory behaviour. An extreme example are partial migrants, where some individuals remain in close proximity of their breeding site while

others travel long distances (Chapman et al. 2011). But also in populations where all individuals migrate, inter-individual migration distance can vary thousands of kilometres (Alves et al. 2012b, Carneiro et al. 2019). For example, sanderling *Calidris alba* breeding in Greenland are found from the coasts of the North Sea to southern Africa during the wintering season (Reneerkens et al. 2009) and lesser black-backed gull *Larus fuscus* breeding in the Netherlands spend the winter between Britain and West Africa (Shamoun-Baranes et al. 2017). Hence, breeders from the same area can disperse across wide geographical ranges and distinct climatic regions in the non-breeding season. Across such large wintering distributions, weather conditions (Castro et al. 1992), habitat and food availability and quality (Piersma et al. 1993, Marra and Holmes 2001, Mathot et al. 2007) will vary, creating distinct costs and benefits for individuals by providing particular conditions for energy intake and expenditure, which ultimately can result in distinct energetic balances (Alves et al. 2013). However, in order to reach these areas the requirements for migration are also likely to differ and individuals might trade-off a longer migration distance (and its associated time and energetic costs and risks) with more favourable conditions at the wintering area (Alves et al. 2013).

In addition, the conditions experienced during a given stage of the annual cycle may not only influence individuals' current state but also affect their performance in subsequent stages (O'Connor et al. 2014). Carry-over effects have been reported for several taxa (reviewed by Harrison et al. 2011) and across wide temporal and spatial scales (Senner et al. 2015). For example, the quality of the wintering site was shown to affect spring departure date in American redstarts *Setophaga ruticilla* (Marra 1998) and spring arrival date in Icelandic black-tailed godwit *Limosa limosa islandica* (Alves et al. 2013). By arriving earlier, Icelandic godwits occupied higher quality breeding territories than later arriving conspecifics (Gunnarsson et al. 2005, Alves et al. 2013, 2019) and likely started nesting earlier, increasing their chances of breeding successfully as timing of breeding is often correlated with fledging success (geese: Bêty et al. 2004, passerines: Norris et al. 2004, raptors: Sergio et al. 2007, waders: Alves et al. 2019). The effect of wintering site quality on breeding performance can also operate through individual body condition. Females wintering in a higher quality site might be in better condition than other females upon arrival at the breeding sites and pre-breeding body condition can influence egg size (Styrsky et al. 2002, Smith and Moore 2003, Sorensen et al. 2009). Larger eggs, in turn, tend to hatch higher quality offspring (Krist 2011). Some studies, however, also report an absence of carry-over effects, when these could be expected. For example, in collared flycatchers *Ficedula albicollis* winter site quality had no effect on the following laying date (Briedis et al. 2018) and in Hudsonian godwits *Limosa haemastica* no effect carried over from one breeding season to the next (Senner et al. 2014). Hence, trade-offs between life-history decisions, such as winter location, and associated carry-over effects have the potential to influence individual fitness in migratory species, but quantifying such effects on breeding performance at the individual level is challanging and remains poorly understood.

The Icelandic whimbrel *Numenius phaeopus islandicus* is a long-distance migrant which breeds mainly in Iceland and spends the wintering season in coastal areas from temperate regions in south-

west Europe to tropical areas in Benin and Togo (Gunnarsson and Guðmundsson 2016, Carneiro et al. 2019). Most tracked individuals migrated to the Guinea-Bissau/Guinea-Conakry region (Gunnarsson and Guðmundsson 2016, Carneiro et al. 2019), where the Bijagós Archipelago (in Guinea-Bissau) hosts important numbers of whimbrel during the boreal winter (thousands to tens of thousands; Dodman and Sá 2005, van Roomen et al. 2015), and is recognized as one of the two most important sites for wintering waders in west Africa (van de Kam et al. 2004, Campredon and Catry 2016). The other one is the Banc d'Arguin, in Mauritania, where large numbers of whimbrels also spend the winter (thousands to tens of thousands; van Roomen et al. 2015, Araujo and Campredon 2016, Oudman et al. 2017). While in autumn all Icelandic whimbrels fly non-stop to the wintering area, two migratory strategies have been identified in spring: a direct strategy, when individuals perform a single flight; and a stopover strategy, when individuals perform one flight to a stopover area, usually in Britain and Ireland, and another flight from there to Iceland (Alves et al. 2016, Carneiro et al. 2019).

Here, we investigate range wide energetic trade-offs and associated carry-over effects of wintering area conditions in the breeding season, at the individual level. We first (1) calculate the energetic balance achieved at three wintering areas, each located in a distinct climatic region and at different distance from Iceland: Tejo Estuary in Portugal – temperate climate –, Banc d'Arguin in Mauritania – arid climate – and Bijagós Archipelago in Guinea-Bissau – tropical climate. Next, we (2) use flight range models to estimate the migration flight costs between each wintering area and Iceland, assuming a direct or a stopover strategy. Finally, we (3) test the effect of laying date on fledging success in this population, before investigating carry-over effects of winter condition into breeding performance in the form of timing of laying and breeding investment (egg volume); and (4) evaluate the effect of wintering conditions on survival (through return rates). Most Icelandic whimbrels spend the winter in the Bijagós Archipelago region (Carneiro et al. 2019), hence we hypothesise that individuals wintering here achieve a higher energetic surplus and that the lowest values should be recorded in the Tejo Estuary, where low numbers winter (few hundred; Alves et al. 2012), suggesting a trade-off between migration distance and winter energetic balance. Consequently, we expect that individuals migrating from the furthest wintering area may arrive and lay earlier than individuals migrating from closer but lower quality areas (Alves et al. 2013). This may be advantageous as we anticipate higher fledging success for earlier laying dates given the short breeding period of whimbrels in Iceland. Finally, by wintering in higher quality sites, females might achieve higher body condition (Marra 1998) and lay larger eggs (Sorensen et al. 2009).

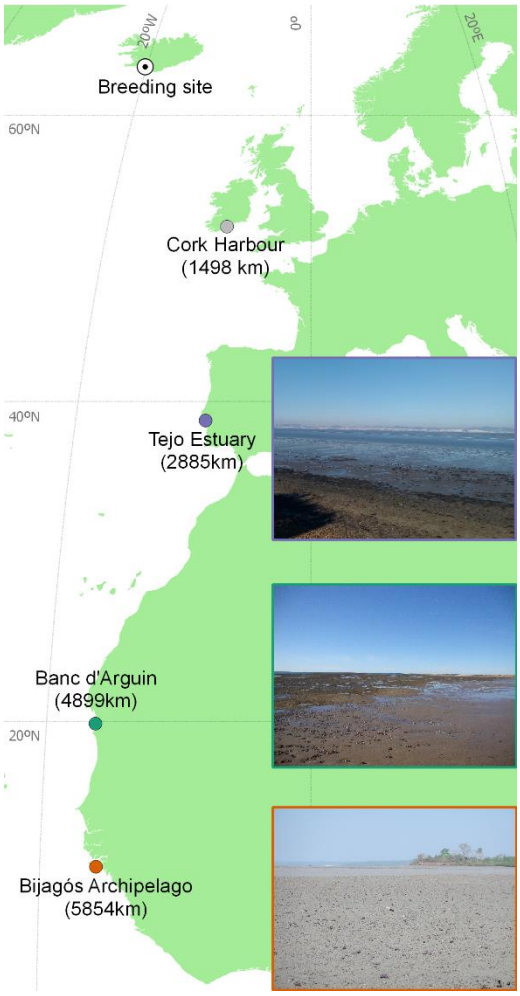


Figure 1. Location of the sampled winter areas (Bijagós Archipelago in Guinea-Bissau, Banc d'Arguin in Mauritania and Tejo Estuary in Portugal), a likely site used for spring stopover in South Ireland (Cork Harbour) and the breeding study site in Iceland. Great circle distance to the breeding site is shown between parentheses for each non-breeding location.

Methods

Study areas

Winter fieldwork was carried out in the Tejo Estuary (Portugal, 38.76°N 8.96°W, hereafter Tejo), the Banc d'Arguin (Mauritania, 19.87°N 16.30°W) and the Bijagós Archipelago (Guinea-Bissau, 11.30°N 15.85°W, hereafter Bijagós; Fig. 3.1). Tejo is a large estuary comprised mostly by mud- and sandflats and sand and rocky beaches with a temperate climate. The Banc d'Arguin, although located in the tropical region, has not a hot and tropical climate but arid and milder, as it lies on the edge of the Sahara desert and is influenced by ocean upwelling (Wolff and Smit 1990). Shorebird habitat here is mostly comprised of intertidal mudflats with varying levels of seagrass and narrow sandy beaches. The Bijagós has a tropical savannah climate and wader habitat is mostly barren mudflats, extensive mangrove areas, sandy beaches, a few rocky shores and intertidal sandflats. A few hundred whimbrels spend the winter in the Tejo (Alves et al. 2012a, Lourenço et al. 2018) while in Banc d'Arguin and Bijagós thousands to tens of thousands are counted during the winter (Dodman and Sá 2005, Oudman et al. 2017). Data was collected during the winters of 2015-2016 to 2017-2018 in the Tejo (October to March), 2016-2017 in the Banc d'Arguin (January and February) and 2015-2016 in the Bijagós (January and February). Breeding season fieldwork (May-June) was carried out in the southern lowlands of Iceland (63.8°N; 20.2°W), between 2015 and 2017.

Foraging behaviour and time budgets

At each wintering area, individual whimbrels were randomly selected while foraging and one-minute focal observations were carried out, in daylight, using a Swarovski ATS 65 HD spotting scope, to record instantaneous intake rate, ingested prey types and prey sizes (see Appendix 3.1 for prey type and size categories). When the focal individual stopped foraging for a brief period during the observation, such periods were recorded and subtracted from the total observation time. When the

total foraging time within a focal observation was less than 50 s, the observation was excluded from further analyses.

In order to determine the foraging time per tidal cycle, two types of observations were conducted: scans and focal observations. Scans consisted of recording the proportion of individuals foraging by quickly inspecting each individual in a flock (Alves et al. 2013). These were performed when a minimum of 10 individuals were observable in the Banc d'Arguin and the Bijagós, and five in the Tejo. When the number of observable individuals in the area did not allow for scans, focal observations of 10 minutes were conducted and the proportion of time during this period allocated to foraging was recorded. Both types of observations were made from dawn to dusk in order to include all tide states and daytime hours. The proportions of foraging calculated from both observation types were pooled into hourly intervals, in relation to tide stage, and converted to the proportion of time foraging during that hour (Altman 1974).

Net Energetic Intake Rate

Prey items encompassing the range of the sizes consumed by whimbrel were collected at each wintering area and transported to the lab to determine the Ash Free Dry Mass (AFDM; see Appendix 3.1 for details on prey collection, preservation and determination of AFDM). The net energetic intake rate (NEIR) was calculated following Alves et al. (2013), as NEIR = IR*FP*EP*AE, where IR is the instantaneous intake rate (gAFDM/h), FP the average daily foraging period (h), EP the energetic content of prey (kJ/g) and AE the assimilation efficiency (% of AFDM). FP was calculated considering foraging activity during one (i.e. ca. 12h) or two tide cycles (i.e. ca. 24h). Following Zwarts and Blomert (1990), we considered an EP of 21 kJ/g and an AE of 43.3%.

Energetic thermoregulatory costs

Energetic costs at each wintering area were calculated following Wiersma and Piersma (1994), by parameterizing the heat loss model for whimbrels (breast height = 0.17m, n = 2; body mass = 382g, 460g, 427g, sampled at each winter site, Tejo (n = 10), Banc d'Arguin (n = 14) and Bijagós (n = 10), respectively). This model allows the estimation of the maintenance metabolism (M_{maint}), given three weather parameters (air temperature, wind speed and solar radiation) and micro-habitat use (e.g. as measured by time-budgets). When the M_{maint} is higher than the basal metabolic rate (BMR), individuals incur an extra energetic cost above this rate. BMR was calculated following Kersten and Piersma (1987) for Tejo and Kersten et al. (1998) for Banc d'Arguin and Bijagós as BMR is different for individuals of the same species in temperate and tropical areas. Each winter period was considered between the 1st of September and the 31st of March, for the purpose of estimating thermoregulatory costs. M_{maint} was calculated for each winter when the observations were carried out, being averaged in the Tagus across the three winters when the observations were made (2015/2016 to 2017/2018). Weather hourly data were retrieved from https://darksky.net/dev (air temperature at 183 cm above ground, in °C, and wind speed at 10 m above ground, in m/s) and

radiation data from http://www.soda-pro.com/web-services/radiation/cams-radiation-service (global irradiation on horizontal plane at ground level, in Wh/m^2).

Migration flight costs

In order to calculate flight costs of migration we used Flight (ver. 1.25, Pennycuick 2008), for which data on wing span, wing area, body mass, muscle fraction and fat fraction are required. These were recorded from whimbrels in the breeding area (Table 3.1). For each individual, the wing span was measured to the nearest mm, the right wing traced and the wing area calculated following Pennycuick (2008). Flight muscle fraction was measured from two dead individuals (road kills) found fresh in Iceland. Both flight muscles were removed and their mass recorded to the nearest mg. We estimated fat fraction by running the flight model with the above parameters and considering the body mass fraction lost by the heaviest individual recorded in the population (601g) flying until reaching the body mass of the lightest (298g), i.e. with no fuel reserves (see deatails in Pennycuick 2008). The body mass (to the nearest gram) of the heaviest bird was measured just prior to departure from Iceland, on the 17th of August (average departure is 12th August, Carneiro et al. 2019) and of the lightest upon its arrival to Iceland, on the 8th of May (average arrival is 8th May, Carneiro et al. 2019). Migration flight costs were estimated for the great circle distance between winter, stopover and breeding sites (Table A3.1.2). In the case of stopover strategy, the total flight cost was calculated as the sum of the cost to migrate to Ireland from each winter location and the cost of flying from there to Iceland, i.e. assuming a new departure from the stopover location with full reserves. Models were run with default parameters in Flight as described by Pennycuick and Battley (2003), except air density that was set for a starting altitude of 0 m and a cruising altitude of 1500m (Alves et al. 2016).

	Mean	n
Wing span (m)	0.868	35
Wing area (m^2)	0.085	35
Body mass (kg)	0.601	1
Fat fraction	0.371	-
Muscle fraction	0.18	2
Cruising altitude	1500	-

Table 3.1. Parameters used to estimate migration flight costs of Icelandic whimbrels, sampled in South Iceland, used in software Flight 1.25 (Pennycuick 2008).

Linking winter site with individual breeding performance

Laying date was recorded by back calculating from the incubation stage, measured through egg floatation (Liebezeit et al. 2007), or from hatching date (assuming 25 days of incubation starting on last egg laid; Carneiro et al. submitted). Eggs were measured to the nearest 0.1 mm and their volume calculated as length*breadth^2*0.509 (Hoyt 1979). Broods were regularly monitored until fledging (27 days of age) and fledging success recorded as fledged young or not. Adults were caught on the nest in the breeding areas, as described in Carneiro et al. (2019). For each captured individual, wing and tarsus-toe lengths (to the nearest mm) and body mass (to the nearest g) were recorded and a blood sample collected from the brachial vein and stored in 96% ethanol. Sex was either determined from biometrics (n = 148) following Katrínardóttir et al. (2013), molecularly (n = 13) as described in Katrínardóttir et al. (2013), or by direct observation of behaviour (n = 9; e.g. copulating position,

assuming that males were on top). Given that most whimbrels perform a complete moult in the wintering grounds (Prater et al. 1979), three to five breast feathers were also collected from each individual and used to infer the wintering location though stable isotope analysis of Carbon and Nitrogen (Catry et al. 2015; see Appendix 3.1 for analysis details).

A linear discriminant analysis (*lda* function from R package MASS; Venables and Ripley 2002) was used to assign a winter location to each individual based on δ13C and δ15N. Three winter regions were considered and named after the respective climatic region: temperate (including Portugal, South Spain and north Morocco), arid (including Mauritania and north Senegal) and tropical (Guinea-Bissau, Guinea-Conakri and Sierra Leone). We used 52 known wintering locations from geolocator data (Carneiro et al. 2019, unpublished) and ring recoveries (Gunnarsson and Guðmundsson 2016, unpublished) to define the prior probabilities in the linear discriminant analysis. The training set was comprised of 75 data points from 31 tracked individuals with known wintering location caught in Iceland and from 35 individuals caught in the wintering areas (Tejo, Banc d'Arguin and Bijagós) between October and February. Individuals were only assigned to a given winter area when the probability of group membership was ≥ 80%, and otherwise excluded.

Data analysis

To test the effect of winter region on laying date (number of days after the 1st of May), a linear mixed model (LMM) was constructed with winter region as fixed effect and individual as a random effect, using only females. To assess the effect of laying date on fledging success (binary: fledged young or not), we constructed a logistic regression with laying date (at nest level) and year as explanatory variables. Second breeding attempts (n = 10) were also included, as young can fledge from either breeding attempt. To investigate the effect of winter region on breeding investment, we used females and, in order to control for body size variation, we calculated the relative egg volume (i. e. average egg volume from the clutch divided by female tarsus-toe length) as an explanatory variable. Although return rates tend to underestimate survival, they are still a useful proxy (Méndez et al. 2018) and were calculated as the percentage of whimbrels (with known wintering region) observed in a given year out of the total present in the previous year. Data were analysed in R (R Core Team 2018) and results are shown as mean ± se, unless otherwise stated.

Results

Foraging behaviour and energetic balance

A total of 149, 516 and 519 focal observations of intake rates were made in Tejo, Banc d'Arguin and Bijagós, respectively. Whimbrels had an average intake rate of 5.27 ± 1.39, 13.34 ± 1.63 and 21.47 ± 2.09 gAFDM h^{-1} and a total foraging time per tidal cycle of 4.81, 5.15 and 4.61 hours in Tejo, Banc d'Arguin and Bijagós, respectively (Fig. 3.2A). Given their site-specific intake rate, foraging period, energetic content of prey and assimilation efficiency, the NEIR was estimated to be lowest in the Tejo. In the Bijagós, NEIR was 1.4x higher than in the Banc d'Arguin and 3.9x higher than in the Tejo (Fig. 3.2B).

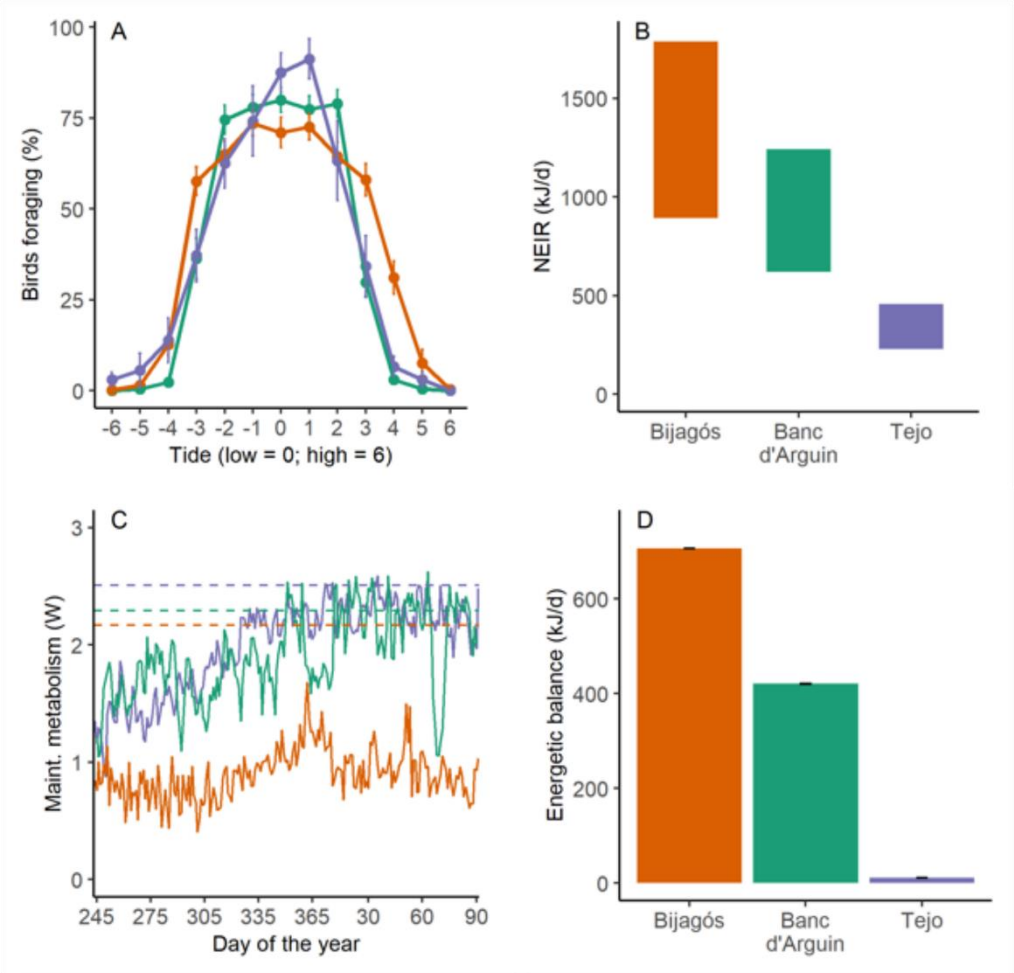


Figure 3.2. Variation among three major wintering locations of Icelandic whimbrel, spread across the winter distribution range - Bijagós (orange), Banc d'Arguin (green) and Tejo (purple) - in: (A) mean percentage (±SE) of time spent foraging each hour across the tidal cycle (low tide = 0; high tide = 6 or -6); (B) estimated range of daily net energetic intake rate, considering foraging during one (minimum) or two tidal cycles (maximum); (C) daily variation on maintenance metabolism throughout the winter (1st September = 244; 31st March = 90; the dashed line notes the site specific basal metabolic rate, above which extra thermoregulatory costs occur, M_{maint}); (D) daily (mean ± SE) energetic balance which is possible to achieve at each wintering area during one tidal cycle.

Whimbrels in the Bijagós never incur energetic costs above BMR to maintain their body temperature, whereas in the Banc d'Arguin and Tejo, this occurs in 20.6% and 9.7% of the winter days, respectively (Fig. 3.2C). The daily energetic balance (i.e. NEIR minus the maintenance metabolism) differed significantly among sites (Kruskal-Wallis H(2) = 987.44, $p < 0.001$), with whimbrels in the Bijagós experiencing on average an energetic surplus of 706.1 ± 0.0 kJ/day, followed by 420.7 ± 0.4 kJ/day in Banc d'Arguin and 11.0 ± 0.2 kJ/day in Tejo (considering daytime foraging only; Fig. 3.2D).

Migratory flight costs

The energetic cost of a direct flight from the Bijagós to Iceland is 7510 kJ, whereas from the Banc d'Arguin and Tejo is 6610kJ and 4400kJ, respectively. If individuals stopover in Ireland, the migration distance increases and the total energetic flight costs rise to 8470kJ, 7510kJ and 4870kJ, respectively (Fig. 3.3), of which 2460kJ is the energy necessary to fly from Ireland to Iceland.

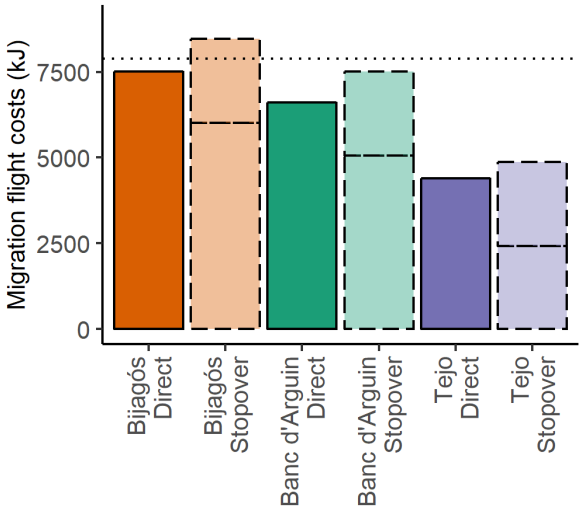


Figure 3.3. Estimated migration flight costs between three wintering areas and the Icelandic breeding grounds, following a direct (bars delimited by solid margin) or a stopover migration strategy (faded colour with bars delimited by dashed margin); in the later, the horizontal line shows the energy required to reach the stopover site (below the line) and that required for the second leg of the journey in spring (above the line); the horizontal dotted line indicates the maximum amount of fuel an individual whimbrel is estimated to store.

Linking winter site with breeding performance

It was possible to assign 149 whimbrels to one of the main winter regions using the linear discriminant analysis on stable isotope data (Fig. A3.1.2). Adding the tracked birds, the wintering region is known for a total of 180 individuals. Most whimbrels wintered in the tropical region (Bijagós Archipelago; 159 individuals), while 20 spent the winter in the arid region (Banc d'Arguin) and one in the temperate region (Tejo). Fledging success decreased with laying date (Fig. 3.4, Table 3.2), but we found no effect of wintering region on laying date, nor of wintering region on relative egg volume (Fig. 3.4, Table 3.2). Similarly, return rates were similar among sites, when considering those with a reasonable sample size (i.e. >10 individuals; 2016: 50.8%, 75% and 100%, for the Bijagós Archipelago (n = 59), Banc d'Arguin (n = 4) and Tejo (n = 1), respectively; 2017: 55.7%, 50% and 100%, for the Bijagós Archipelago (n = 79), Banc d'Arguin (n = 14) and Tejo (n = 1), respectively).

Table 3.2. Linear mixed models results testing differences in (A) timing of breeding (laying date) and (B) breeding investment (relative egg volume) among wintering regions and sex. And (C) logistic regression testing the effect of laying date and year on fledging success; estimates for site are in relation to Bijagós Archipelago and for year in relation to 2015.

	Linear Mixed Models								
	Fixed effects						Random effects		
		Estimate	SE	df	*t*	*p*		Variance	SD
A *n = 98*	Intercept	32.34	0.959	78.339	33.725	< 0.001	Individual	46.07	6.79
Laying date	Banc d'Arguin	-0.74	2.828	83.752	-0.26	0.795	Residual	24.68	4.97
	Tejo Estuary	-9.84	7.70	45.14	-1.277	0.208			
B *n = 97*	Intercept	481.64	3.67	81.29	131.13	< 0.001	Individual	859.5	29.32
Relative egg volume	Banc d'Arguin	-17.85	10.69	82.84	-1.67	0.0987	Residual	148.6	12.19
	Tejo Estuary	7.57	30.78	69.05	0.25	0.8066			

	Logistic regression				
		Estimate	SE	z	*p*
C *n = 235*	Intercept	1.37	0.78	1.76	0.079
Fledging success	Laying date	-0.07	0.02	-3.07	**0.0021**
	Year 2016	-0.31	0.40	-0.79	0.4304
	Year 2017	-0.22	0.39	-0.55	0.5793

Discussion

Understanding how individual trade-offs and carry-over effects along the annual cycle influence fitness is fundamental to unravel population dynamics (Norris 2005, Marra et al. 2015). However, such data is particularly challenging to collect in long-distance migrants, as it requires individual tracking and sampling across wide regions, with most studies tending to focus on singular parts of the annual cycle (e.g. breeding; Marra et al. 2015). By studying Icelandic whimbrels, we provide an annual cycle perspective of a long-distance migrant, linking breeding parameters and migration costs to wintering locations across the entire distribution range. Icelandic whimbrels trade-off higher costs of migration with more favourable wintering conditions, in terms of energetic balance. By migrating further to lower latitude areas, whimbrels experience lower thermoregulatory costs and higher net energetic intake rates, resulting in a more positive energetic balance during the winter. However, these differences in wintering site quality did not appear to carry-over to the breeding season in terms of measurable effects on subsequent laying dates (and, consequently, fledging success), egg volume or return rate, for individuals wintering across the population range.

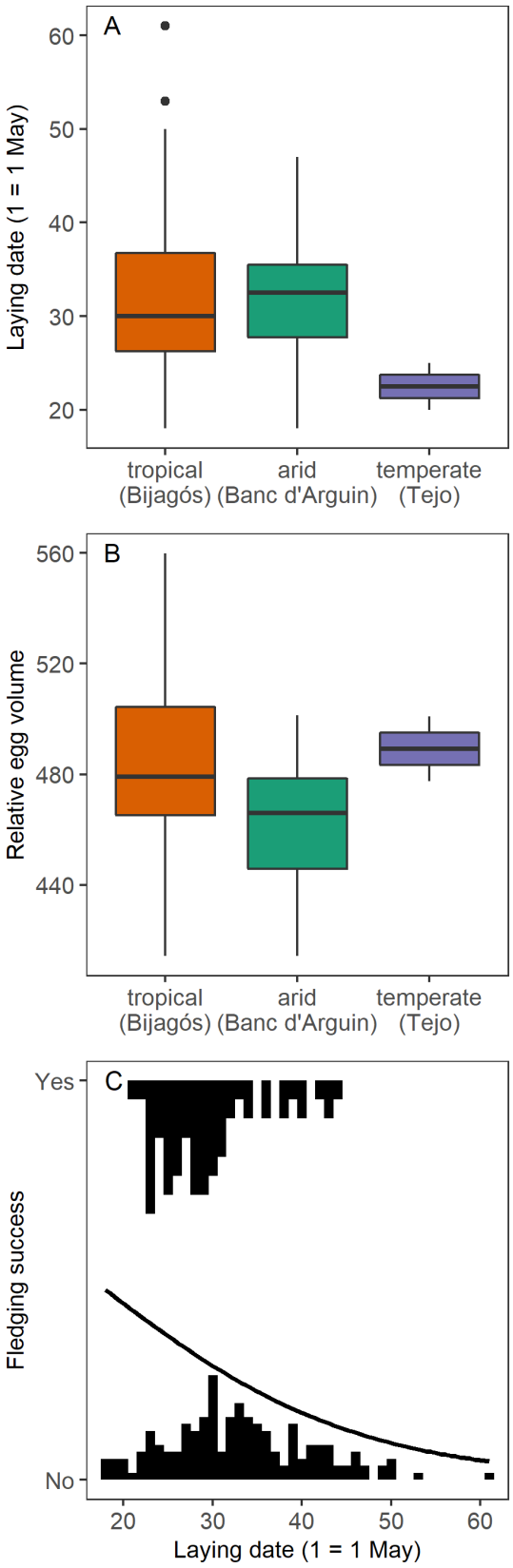


Figure 3.4. (A) Laying date (day since 1st of May) and (B) relative egg volume (mean egg volume, in mm^3, divided by tarsus-toe length, in mm) of female whimbrels that spend the winter in a tropical (A: n = 86; B: n = 85), arid (A: n = 10; B: n = 10) or temperate climate region (A: n = 2; B: n = 2); (C) logistic curve of fledging success in function of laying date (day since 1st of May); boxes show the median and 25% and 75% quartiles, whiskers extend up to 1.5 times the inter quartile range from the hinge and points beyond that are individually marked in black.

Whimbrels wintering in the Bijagós Archipelago (tropical region) achieved the most positive energetic balance, followed by Banc d'Arguin (arid region) and Tejo (temperate region). In other words, energetic balance was more positive with decreasing latitude, which is in line with the observed patterns in other avian migrants, where energetic living costs are lower at southerly latitudes (sanderling, Castro et al. 1992; bar-tailed godwit *Limosa lapponica*, Drent and Piersma 1990; black-tailed godwit, Alves et al. 2013). The values recorded in this study were relatively high when compared to others: for example, we recorded an average intake rate of 13.34 gAFDM/h in the Banc d'Arguin, while Zwarts and Dirksen (1990) recorded ca. 3.6 gAFDM/h in 1986-88. Turpie and Hockey (1997) recorded a daytime NEIR between 154 and 481 kJ in South Africa (33°S), Mauritius (20°S) and Kenya (3°S), during the winters of 1991 to 1993, while in our study daytime NEIR ranged from 229 to 893 kJ. To some extent such differences might be explained by temporal and spatial variation, but also protocol differences (such as prey preservation method and the assimilation efficiency considered; Leuven et al. 1985, Wetzel et al. 2005). Nevertheless, since the same protocol was applied to all sites in our study, the relative differences observed between studied sites must parallel biological variation.

In accordance to our hypothesis, whimbrels traded-off costlier migrations with wintering in a more favourable area. Besides basal metabolism and thermoregulation, daily activities (such as foraging and flying) also require energy. If we assume that whimbrels have an average daily energy expenditure (DEE) of 2.5 times their BMR (Bryant and Tatner 1991), then the energetic surplus should be sufficient in the Bijagós and Banc d'Arguin (DEE = 468.9 and 494.9 kJ/d, respectively), but not in Tejo. In this winter location the DEE is estimated at 541.9 kJ/d but the energetic intake is only 229.0 kJ/d. Even if individuals forage during the night, in the Tejo, the energetic intake (489.1 kJ/d) will still be lower than DEE. It is possible, and likely, that whimbrels forage during the night in the Tejo, as other waders do (Lourenço et al. 2008), and in such case the negative balance would be relatively low, i.e. ca. 83 kJ/d. Naturally, individuals cannot survive with a negative energetic balance, suggesting that mortality may be higher in this site, but it should also be considered that the estimated energetic intake is an average value involving several fudge factors (e.g. DEE, assimilation efficiency, energetic content of prey). It also illustrates that the Tejo seems to be the most difficult site for whimbrels to achieve their daily energetic requirements, when compared to furthest wintering sites from Iceland, as the Banc d'Arguin and Bijagós.

The consequences of a trade-off between migration distance and wintering site might go beyond immediate advantages upon arrival at winter location or during the wintering period. Spending the winter where energetic surplus is higher, might allow individuals to fuel for the first migratory flight in spring at a faster rate and thus reduce migration duration (Carneiro et al. 2019). For example, if we assume that the extra energy above DEE can be allocated to migration fuel, in the Bijagós and Banc d'Arguin individuals would require 18 and 53 days to be ready for a direct flight to Iceland, respectively, resulting in considerable differences of migration duration and speed. However, it should be noted that for the Bijagós these figures seem unlikely as it suggests that individuals experience a fuel deposition rate of 4.87% LBM, which is considerably higher than the maximum individual value recorded (3.55% LBM, Lindström 2003). Spare energy can also be used for other activities. In a tropical climate individuals are more likely to suffer heat stress than at higher latitudes and therefore allocate energy to heat reduction behaviour (Battley et al. 2003). Conversely heat stress is unlikely to occur in the Tejo and Banc d'Arguin, where air temperatures are lower. In addition, whimbrels in the Bijagós (tropical area) might move larger distances between feeding and roosting areas, as intertidal areas are much larger than in the other two locations. Site specific differences and associated behaviours may in part explain the higher energetic intake in that area.

Carry-over effects have been widely reported in several taxa (reviewed by Harrison et al. 2011) across wide temporal and spatial scales (Senner et al. 2015). In birds, the quality of the wintering area has been shown to affect subsequent stages in the annual cycle and individual survival (e.g. Marra et al. 1998, Gunnarsson et al. 2005, Alves et al. 2013). Similarly, we expected that Icelandic whimbrels wintering in more favourable sites would arrive earlier into Iceland, lay earlier and/or lay larger eggs, and possibly show differences in return rates. Although the arrival dates are unknown, the laying dates of individuals wintering in different regions did not differ, therefore no effect on

fledging success was apparent. Additionally, females that spent the winter in different regions also did not vary in average egg volume, suggesting that egg investment was not influenced by conditions experienced in the previous season. However, the period that females have in Iceland before laying (mean: 19 ± 1.02 days; n = 25; Chapter 5) might be enough to dissipate winter effects on body condition, and individual consistency in egg size may further prevent detection of such effects. Also, no differences in return rate are evident, when considering sites with appropriate sample size. Perhaps carry-over effects could more likely be expected to arise in birds wintering in the least favourable wintering site, i.e. Tejo, but unfortunately sample size prevented a suitable evaluation.

Similarly to Hudsonian and bar-tailed godwits (Conklin and Battley 2012, Senner et al. 2014), Icelandic whimbrels breed at high latitudes and perform long distance flights between the breeding and wintering sites (Alves et al. 2016, Carneiro et al. 2019). These characteristics render the apparent lack of carry-over effects from the wintering site unsurprising. Given their extreme life-history, the range of individual quality in the population might be truncated due to a high selective pressure on young individuals and their annual schedule might allow the dissipation of inter-seasonal effects (Conklin et al. 2017). However, whimbrels have a typical lifespan of 11 years, can live more than two decades (Robinson, 2018), and are philopatric in winter (Mallory 1982, Zwarts 1990, McNeil and Rompre 1995). Hence, differences among individuals using different wintering sites through their lives may only become evident if assessed over several years.

Wintering site quality might have an influence in other ways. For example, whimbrels perform a complete feather moult at the wintering sites (Prater et al. 1979), which is energetically costly (Lindström et al. 1993), and if performed under limiting energetic conditions might lead to low feather quality and influence flight performance (Swaddle et al. 1996). Furthermore, if wintering site quality leads to a delayed spring migration and late arrival into Iceland, individuals might divorce (Gunnarsson et al. 2004) and fail to breed, an effect that would go undetected in this study as wintering region was only assigned to nesting birds. Another layer to consider is the possibility of a seasonal matching of habitat quality and individual fitness, when the same individuals tend to use high quality sites both on the breeding and wintering areas (Gunnarsson et al. 2005). Our breeding study area had a relatively high density of pairs (20.1 ± 2.4 pairs/km^2; range 4 - 38 pairs/km^2 in Katrínardóttir et al. 2015), where individual quality might be high. Hence, one would potentially find a higher percentage of individuals that winter in suboptimal sites (e.g. Tejo) breeding in lower density (and lower quality) areas in Iceland.

To conclude, the population dynamics of Icelandic whimbrels seem unlikely to depend on the quality of the wintering sites (estimated as the energetic balance achieved), since individuals using different wintering regions do not appear to differ in breeding output and return rates to breeding grounds. However, given some life-history traits of whimbrels, such as winter site philopatry and longevity, it is possible that variation in fitness may only become evident if individual performance is assessed over several years. Whimbrels seem to favour wintering locations where conditions are more

favourable, as the variation on wintering distribution abundance, reflects the differences in winter site quality, with a larger number of birds wintering in the tropical and arid areas and only a few in the periphery of the distribution (van Roomen et al. 2015). Despite the apparent lack of differences in fitness between birds from distinct wintering sites, the tendency to use energetically favourable wintering sites even if further from the breeding sites, is in accordance with other systems of long-distance migrants (e.g. sanderlings Castro et al. 1992, black-tailed godwits Alves et al. 2013). This points towards the idea that the most favourable wintering site can be located where living costs are cheaper (and survival likely higher), independent of distance to the breeding grounds (Greenberg 1980). However, further knowledge on fitness and survival consequences arising from using different wintering sites and their impact on population dynamics remains necessary to pursue.

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Appendices

Appendix 3.1

Prey type and size categories

Given that the wintering diet of Whimbrel is mostly comprised of crabs (Zwarts and Dirksen 1990), the following prey types were considered: European Green Crab *Carcinus maenas*, West African Fiddler Crab *Uca tangeri* (consumed whole, just carapace, or male without big cheliped), swimming crab *Callinectes sp.*, Mottled Shore Crab *Pachygrapsus transversus*, Panopeus/Mennipe *Panopeus africanus* or *Mennipe nodifrons*, non-identified crab, crab leg and other prey (shrimps, *Balsscallichirus* sp., worms and non-identified items). West African Bloody Cockle *Senilia senilis* was additionally considered, given its recent importance for Whimbrels wintering in Banc d'Arguin (Carneiro et al. 2017).

Prey size was estimated as categories in relation to bill length (Zwarts and Dirksen 1990), considering a bill of 85 mm (average 85 ± 0.4 SE mm, n = 249). Each size category corresponds to 10.6 mm intervals (category 1, 1-10.6 mm, i.e. ca. < 1/8 bill length; category 2, 10.6-21.3 mm, i.e. ca. < 1/4 bill length, category 3, 21.3-30.9 mm, i.e. ca. < 3/8 bill length, category 4, 31.9-42.5 mm, i.e. ca. < 1/2 bill length, category 5, 42.5-53.1 mm, i.e. ca. < 5/8 bill length). For all crab species, carapace width was the considered size and the length of the longest axis size for other prey (e.g. total length in the case of shrimps), except for West African Bloody Cockles where shell width was considered. However, Whimbrels do not always unearth this prey, preventing size to be evaluated (Carneiro et al. 2017). In those cases (68%), we assumed the most frequent size recorded during our observations, i.e., size category 4. The prey size and quantity ingested was converted into AFDM using the equations in table A3.1.1.

Prey collection

Prey items encompassing the range of the size categories were collected at each wintering area where Whimbrels were recorded foraging, preserved in ethanol 70% and taken to the laboratory. However, as ethanol preservation of invertebrates may affect the ash free dry mass (AFDM; Leuven et al. 1985), the most common prey were also preserved dry (European Green Crab *Carcinus maenas*, West African Fiddler Crab *Uca tangeri*; West African Bloody Cockle *Senilia senilis*; swimming crab *Callinectes sp*). Logistic constraints prevented to dry all prey types, but less common

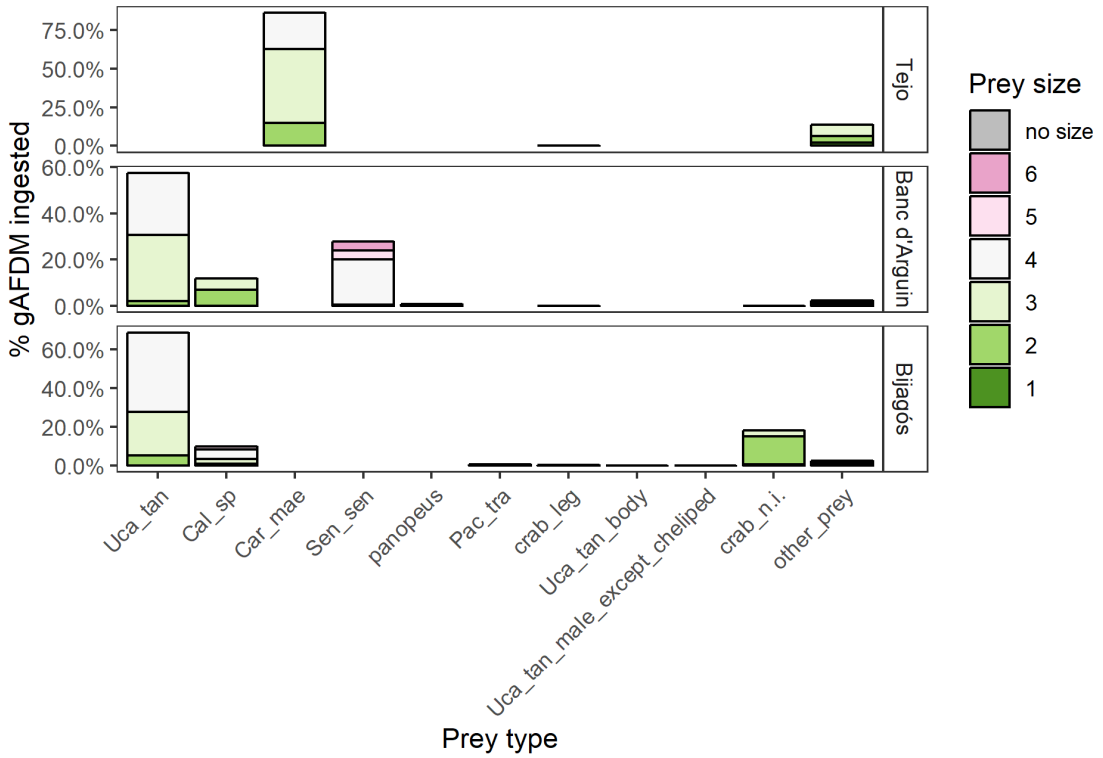

Figure A3.1.1. Percentage of total of prey ingested (in gAFDM) in all observations, by prey category, size and wintering area.

prey were mostly comprised by small size categories (Figure A3.1.1), where the difference in AFDM between ethanol vs. dry preserved is small (for example, for 10mm fiddler crabs the difference is 0.0077 gAFDM; Table A3.1.1).

Determining the Ash Free Dry Mass of prey

In the lab, each prey item was dried at 60°C for 48h, the dry mass recorded, burnt in a muffle furnace at 550°C for 2h, the ash mass recorded and the AFDM content calculated (Zwarts and Blomert 1990).

An exponential regression was fitted to each prey type AFDM against their size (except for crab legs for which a mean value was calculated). To calculate the ingested AFDM per prey, we assumed that Whimbrels consumed on average the mid size within each prey size category (e.g. 15mm for prey size category 2). Whenever possible, the AFDM estimated from dry samples was used. For swimming crab and non-identified crab we used the equations calculated from dried samples to adjust the calculated from ethanol preserved samples (see Table A3.1.1).

Table A3.1.1. Exponential regressions of ash free dry mass (AFDM) as a function of prey size, drawn from samples preserved in ethanol or dried; the values for crab legs are the mean ± SE; CW - carapace width*; SW - shell width.

Area	Prey group	Preservation method	Equation	n	Size range (mm)
Tejo	Carcinus maenas	Dry	ADFM = $0.000006592*CW^{3.463}$	40	9.3 - 47.9
		Ethanol	ADFM = $0.000007021*CW^{3.337}$	39	6.0 - 47.0
Banc d'Arguin	Uca tangeri	Dry	ADFM = $0.00002723*CW^{3.323}$	10	21.1 - 33.2
		Ethanol	ADFM = $0.00000864*CW^{3.465}$	36	4.9 - 41.8
	Callinectes sp.	Dry	ADFM = $0.007183*CW^{1.516}$	8	22.7 - 48.3
		Ethanol	ADFM = $0.00000311*CW^{3.495}$	32	13.4 - 49.7
	Senilia senilis	Dry	ADFM = $0.00001109*SW^{2.904}$	33	7.3 - 87.8
	Uca tangeri body	Ethanol	ADFM = $0.000008573*CW^{3.467}$	27	12.8 - 41.8
	Uca tangeri male expt cheliped	Ethanol	ADFM = $0.0000217*CW^{3.131}$	15	12.8 - 41.8
	Panopeus/Mennipe	Ethanol	ADFM = $0.00004622*CW^{3.009}$	14	5.3 - 38.1
	crab n.i	Ethanol	ADFM = $0.000003939*CW^{3.598}$	107	4.9 - 39.6
		Dry	ADFM = $0.002472*CW^{1.921}$	18	18.6 - 38.8
	crab leg	Ethanol	ADFM = 0.0341 ± 0.0016 (mean ± se)	401	
	other prey	Ethanol	ADFM = $0.0004636*CW^{2.016}$	108	4.9 - 30.0
Bijagós Archipelago	Uca tangeri	Dry	ADFM = $0.0000613*CW^{3.019}$	24	6.6 - 32.9
		Ethanol	ADFM = $0.00008346*CW^{2.829}$	39	5.3 - 30.6
	Callinectes sp.	Ethanol	ADFM = $0.000001998*CW^{3.479}$	26	16 - 42.3
		Dry[1]	AFDM = $0.007183*(CW^{3.479})^{0.436}$		
	Uca tangeri body	Ethanol	ADFM = $0.0002329*CW^{2.510}$	19	14.7 - 30.6
	Uca tangeri male expt cheliped	Ethanol	ADFM = $0.00001219*CW5^{3.343}$	13	14.7 - 30.6
	Panopeus/Mennipe	Ethanol	ADFM = $0.00000493*CW^{3.656}$	16	8.2 - 35.3
	Pachygrapsus transversus	Ethanol	ADFM = $0.00008209*CW^{2.785}$	14	8.2 - 21.2
	crab n.i	Ethanol	ADFM = $0.000003406*CW^{3.738}$	82	5.3 - 29.9
		Dry[1]	AFDM = $0.002472*(CW^{3.738})^{0.514}$		
	crab leg	Ethanol	ADFM = 0.0198 ± 0.0009 (mean ± se)	395	
	other prey	Ethanol	ADFM = $0.00001027*CW^{3.410}$	116	5.3 - 30.0

[1]converted equation using Banc d'Arguin ethanol preserved samples.
*The carapace width of Callinectes sp. does not include the lateral spines.
For the only observation in Tejo where a single crab leg was consumed, the average AFDM value from Banc d'Arguin and Bijagós was used.

Stable isotope analysis

In the lab, feathers were washed with 2:1 chloroform/methanol solvent, left to dry for 24h, clipped into pieces of ca. 2mm and weighed in tin capsules to a total mass of ca. 0.5 mg. The capsules were crimped, loaded into a stacked carousel autosampler system, dropped individually into the reactor and analysed by dynamic flash combustion using a Thermo Flash HT Plus. Tin capsules combust in an exothermic reaction. Nitrous oxides which may be formed during combustion are reduced by Cu to N_2. After removal of H_2O, the N_2 and CO_2 were separated on an isothermal GC column and the 15N/14N and 13C/12C isotope ratios were measured sequentially on a DELTA XP Isotope Ratio MS. Results are shown conventionally as δ values in parts per thousand (‰) relative to VPDB for δ13C and AIR for δ15N.

Conversion of prey ash free dry mass from ethanol preserved to dry

After calculating the exponential regression of ash free dry mass (AFDM) as a function of crab size for dry samples from Banc d'Arguin, the expected relationship for dried Callinectes sp. and crabs n.i. from Bijagós was estimated. This was done by solving the ethanol equation as a function of prey size, replace it in the dry equation and then solving it for the desired prey category, as follows:

Assuming that $\mathrm{AFDMethanol} = \mathrm{a} \times \mathrm{size}^{p}$ and $\mathrm{AFDMdry} = \mathrm{b} \times \mathrm{size}^{q}$, $\mathrm{size} = (\mathrm{AFDMethanol}/\mathrm{a})^{1/p}$.

Then, $\mathrm{AFDMdry} = \mathrm{b} \times (\mathrm{AFDMethanol}/\mathrm{a})^{q/p}$, which equals to $\mathrm{AFDMdry} = \mathrm{b} \times (\mathrm{size}^{p})^{q/p}$

	Breeding site	S Ireland
Breeding site	1498	
Tejo Estuary	2885	1461
Banc d'Arguin	4899	3632
Bijagós Archipelago	5854	4569

Table A3.1.2. Great circle distances (km) between wintering and stopover areas of Icelandic Whimbrels used to calculate cost of migration.

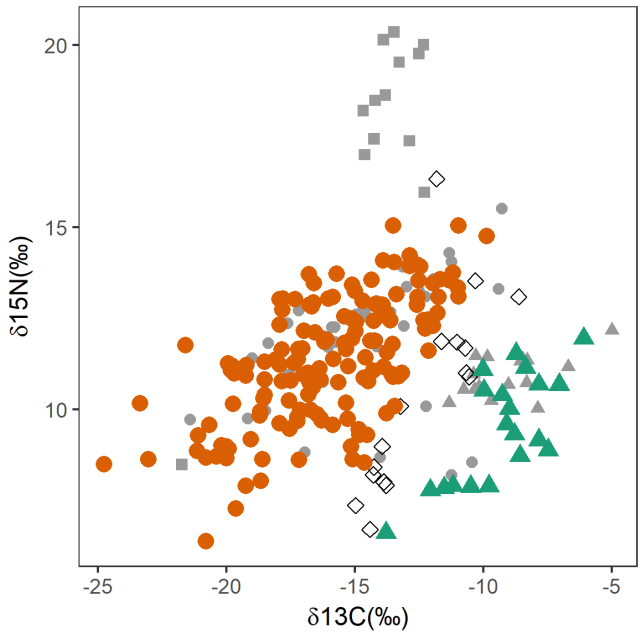

Figure A3.1.2. Stable isotope signal of δ13C and δ15N of the training dataset used in the linear discriminant analysis (in grey) and the wintering region for the remaining individuals, using ≥ 80% assignment probability of group membership; winter regions not assigned represented as empty diamonds; winter regions assigned in orange (tropical) and green (arid); circles: tropical; triangles: arid; squares: temperate.

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CHAPTER 4

WHY ARE WHIMBRELS NOT ADVANCING THEIR ARRIVAL DATES INTO ICELAND? EXPLORING SEASONAL AND SEX-SPECIFIC VARIATION IN CONSISTENCY OF INDIVIDUAL TIMING DURING THE ANNUAL CYCLE

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Previous photo by Camilo Carneiro.
Whimbrel wearing a leg flag with geolocator, Iceland, 21 May 2018.
This geolocator weighs 1 g (only 0.2% of the average body mass of nesting whimbrels in Iceland).

WHY ARE WHIMBRELS NOT ADVANCING THEIR ARRIVAL DATES INTO ICELAND? EXPLORING SEASONAL AND SEX-SPECIFIC VARIATION IN CONSISTENCY OF INDIVIDUAL TIMING DURING THE ANNUAL CYCLE

Abstract

The timing of annual events is key for organisms that exploit seasonal resources, as deviations from optimal timing might result in considerable fitness costs. Under strong time selection, individuals likely have fewer suitable strategies available than when selection is more relaxed, hence both consistency and flexibility might be advantageous depending on the life history or annual cycle stage. For migrants using both the arctic and the tropics during their annual cycle, the faster warming at higher latitudes than elsewhere in the range may lead to mismatches with local environmental conditions. Additionally, while individuals might already be limited in responding to changes at each stage, the potential degree of a given response will likely also be limited by responses at previous stages of the annual cycle.

Contrary to other migratory waders breeding in Iceland, Icelandic whimbrels *Numenius phaeopus islandicus* have not changed arrival dates during the past 30 years, suggesting high individual consistency in spring arrival timing and a potential limitation in responding to a changing environment. After repeatedly tracking 12 individual Icelandic whimbrels at least twice throughout their annual cycle between 2012 and 2018, we investigated individual consistency of spring arrival date and other annual stages and migration strategy, and explored differences between sexes and seasons. Individuals were more consistent on timing of spring than autumn migration, and the most consistent stage was departure from the wintering sites. Timing of laying was the stage that varied the most, and no overall significant difference between sexes was observed, except on spring stopover duration.

While lower consistency in laying dates might allow individuals to track the advancement of spring, consistency at departure from the wintering sites, stopover duration, and arrival into Iceland might limit the degree of advancement. Transgenerational changes in the migratory behaviour of other wader species allows population level responses to a changing phenology, but seems unlikely for Icelandic whimbrels, given the stable dates of spring arrival in this population. Under continuing advancement of spring onset, it is thus important to acquire information on the timing of spring arrival of recruits and on the ontogeny of migration to understand how migratory schedules are defined and might influence responses of long-distance migrants to environmental change.

Introduction

The annual cycle of many animals comprises migratory periods during which individuals travel to exploit seasonally available resources (Newton, 2007). Timing of specific events, such as breeding, is therefore fundamental (Alerstam and Lindström, 1990), but selection for optimal timing of events might not be equally strong between different stages of the annual cycle. Due to the influence that timing of breeding can have on breeding success and thus individual fitness (Drent, 2006; Perrins, 1970), selection on timing during the preceding spring migration is expected to be stronger than in autumn (McNamara et al., 1998). Under strong time selection, the available strategies (e. g. schedules) for individuals are likely to be fewer than when selection is more relaxed and individuals can perform a given task (e. g. migration) over a wider time window (Madsen, 2001; Warnock et al., 2004). Therefore, both consistency and flexibility can be advantageous depending on the life history of a given species (Vardanis et al., 2016).

For migrants breeding in arctic and sub-arctic environments, selection on timing of breeding is expected to be strong, given the relatively short time window with favourable environmental conditions for reproduction. However, climate is changing at a faster pace than some species are able to adjust to (Both and Visser, 2001), and the situation can become more complicated in the arctic, where temperatures are increasing more rapidly than at lower latitudes (Høye et al., 2007; Serreze et al., 2009; Cohen et al., 2014). Whereas individual consistency can differ among distinct annual events (e. g. Conklin et al. 2013, Verhoeven et al. 2019), the performance of individuals at a given stage may also depend on the conditions experienced in previous stages (Harrison et al., 2011; O'Connor et al., 2014). Hence, consistent behaviour at one stage might thus limit the degree of change in the subsequent one. Detailed data throughout the annual cycle (e.g. Senner et al., 2014) is therefore required to understand how individuals and populations might be limited in their capacity to respond to a changing environment (Marra et al., 2015).

Previous research has indicated that most species of waders (Charadrii) breeding in Iceland have been advancing their spring arrival dates (e.g. golden plover *Pluvialis apricaria*, common snipe *Gallinago gallinago*, black-tailed godwit *Limosa limosa*), accompanying the trend of temperature change, but Icelandic whimbrels *Numenius phaeopus islandicus* were an exception (Gunnarsson and Tómasson, 2011, Gill et al., 2014). We update this information by adding nine years of data of first arrival for birds recorded in South Iceland (see Gunnarsson and Tómasson, 2011 for details) and confirm that arrival dates show no significant trends since 1988 for this population (Figure 4.1). Whimbrels are long-lived birds (typical lifespan: 11 years; Robinson, 2018) that are long-distance migrants. The Icelandic subspecies breeds predominantly in Iceland, with an estimated population of 256,000 pairs (Skarphéðinsson et al. 2016), and winters in West Africa (Carneiro et al., 2019; Gunnarsson and Guðmundsson, 2016). In spring, their departure from the wintering sites occurs on the second fortnight of April and arrival into Iceland from late April to early May, with individuals performing one of two migratory strategies: a non-stop flight or two flights divided by a relatively short

stopover; in autumn, migratory movements occur from late June to late August and only the direct flight strategy has been recorded in this season (Alves et al. 2016, Carneiro et al. 2019). Icelandic whimbrels are site faithful to the breeding territory, monogamous, and most reproduce with the same partner from year to year (BWPi, 2006), with males arriving earlier and departing later from breeding sites than females (Carneiro et al., 2019).

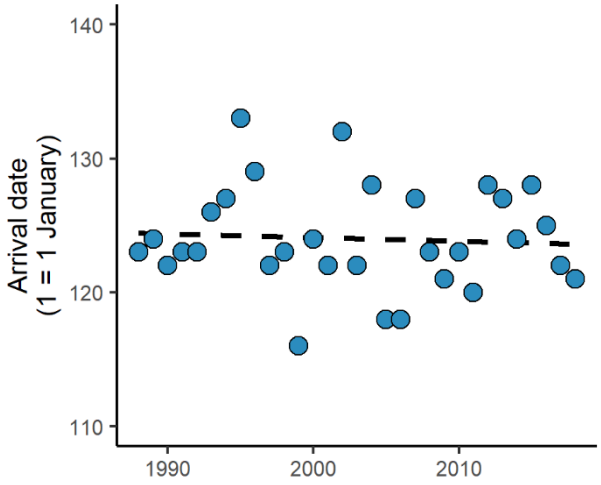

Figure 4.1. Arrival dates of whimbrels into South Iceland in the 31-year period from 1988 to 2018, updated from Gunnarsson and Tómasson (2011), showing no significant trend (day of the year = -0.027 * year + 178.11, n = 31, R^2 = 0.004, p = 0.734).

The low variation of Icelandic whimbrels arrival dates into Iceland and the lack of a population advancement (Figure 4.1) in response to increasing temperatures may suggest consistency of individual spring arrival dates. Individual consistency in this population is currently unknown, but, at the same time, important to unravel in order to understand potential limitations to population-level responses. Hence, we quantified (1) individual timing consistency in arrival dates to Iceland, and at five other annual stages (departure and arrival during autumn migration, departure of spring migration, stopover duration in spring, and laying date) in order to investigate possible constraints to throughout the year; (2) individual consistency in migratory strategy; and tested for (3) seasonal and sex differences in timing consistency. Along with a lack of population variation in spring arrival date, and a higher pressure for breeding timing than for arrival into the wintering sites, we expected higher consistency during spring than autumn migration, but lower consistency in laying dates than during other stages, as this also depends on the schedule of the partner and on their return. For spring migration, consistency might be higher at departure because conditions are likely to be more stable at the wintering sites than at breeding areas, where weather conditions are more variable (as stochastic weather events can reduce food availability and lead to mortality; Vepsäläinen, 1969, Marcström et al. 1979) and the occurrence of a stopover during migration might also influence arrival. However, during autumn, consistency should not vary from departure to arrival due to the direct strategy. Because males arrive earlier than females to defend territories and also attend broods longer (BWPi, 2006), we anticipated that males should show higher consistency on spring migration and less so at autumn departure than females.

Methods

Fieldwork was carried out on whimbrels at breeding grounds in the southern lowlands of Iceland (63.8°N; 20.2°W), between 2012 and 2018. Nests were searched for and upon finding, the incubation stage estimated through egg floatation (Liebezeit et al. 2007), and the laying date was back calculated from stage of incubation. Nests were monitored until hatching and for those that hatched, laying date was back calculated from the hatching date considering an incubation period of 25 days after the last egg laid (mean ± se: 24.8 ± 0.2 days, n = 24 nests found when laying, and hatch recorded). Because whimbrels were individually marked (see below), we were able to identify replacement clutches which were not included in the analyses.

Two hundred and twenty-six adult birds were caught on the nest, using a nest trap (Moudry TR60; www.moudry.cz). Birds were individually marked with a unique metal ring, issued by the Icelandic ringing scheme, and a combination of colour rings. Geolocators were fitted on a leg flag to a subgroup of 86 individuals (number of geolocators deployed per year - 2012: 10; 2013: 3; 2014: 10; 2015: 30; 2016: 40; 2017: 40). The device was replaced whenever possible each breeding season. Sixty-two devices were retrieved one or more years later (number of geolocators retrieved per year - 2013: 5; 2014: 4; 2015: 5; 2016: 14; 2017: 20; 2018: 14). For tags retrieved two or more years later, data on two autumn migrations were recorded. We used the Intigeo-W65A9RJ model from 2012 to 2014 and Intigeo-C65 in the following years (Migrate Technology Ltd). One device stopped logging in mid-winter, another shortly after departure from Iceland, and a third one was damaged and contained no data. Sixty five individuals were sexed using biometrics following Katrínardóttir et al. (2013), 22 molecularly (as in Katrínardóttir et al., 2013), eight through behavioural observation (copulating position, assuming males on top) and two remained undetermined. Geolocator data analysis and determination of individual departure and arrival timings were performed using light, and temperature, conductivity and wet contacts as described in Carneiro et al. (2019). Due to the accuracy of geolocators (Phillips et al. 2004), we considered arrival and departures to/from the general area. For example, spring arrival was arrival into Iceland instead of arrival into the breeding territory (although some individuals have been observed on the breeding territory on the day of arrival into Iceland). We consider stopover any stop during travel between breeding and wintering locations, irrespective of length of stay, site quality or previous or future flight distance and duration (*i.e.* we do not discriminate from staging; Warnock, 2010). Although stops of few hours may be undetected with geolocator data, stopovers of Icelandic whimbrels are usually of several days (Carneiro et al., 2019), with the minimum stopover duration recorded during this study being six days.

Icelandic whimbrels show two migratory strategies in spring: a direct non-stop flight or two flights with a stopover in between (henceforward: “direct” and “stopover”; Carneiro et al., 2019). However, and adding to previous information, during this study one individual was recorded undertaking a stopover during autumn migration. To understand individual consistency in migratory strategy we calculated

the percentage of individuals that changed strategy during the tracking period and the direction of change (i.e. from direct to stopover, from stopover to direct, or both).

Repeatability (*R*) was estimated in a mixed effects model framework, using 1000 bootstrap iterations to estimate the confidence intervals, with R package *rptR* (Stoffel et al. 2017). Given that *R* takes into account both within- and between-individual variances, it does not translate into absolute consistency (see Conklin et al., 2013), and therefore we also calculated the mean individual range (difference between the latest and earliest record for each individual for each stage, in days) and the absolute interannual difference (absolute difference between consecutive years for each individual within stage, in days) in order to better evaluate individual consistency. To test for differences in consistency between stages and sexes, we fit a generalized linear model with absolute interannual difference as the dependent variable and stage, sex, and their interaction as explanatory variables (with family = Poisson due to the positively skewed dependent variable). In this analysis we did not account for the dependency of member of the same pair, because we could have only used those individuals that nested with the same partner in consecutive years, which would result in a reduced sample size. Data were analysed in R (R Core Team 2018) and results are shown as mean ± se.

Results

We recorded individual level data spanning two to seven years, with a median of three years for autumn migration (n = 16 individuals), and two years for spring migration (n = 12 individuals) and for laying date (n = 70 individuals). Hence, autumn migration, spring migration and laying date were recorded during a median of 27%, 18%, and 18%, and up to 54%, 46% and 64%, of whimbrels typical lifespan (Robinson, 2018), respectively. During the present study, one individual was recorded making a stopover during autumn for the first time. In that season, one individual (out of 16) switched strategy between years, from a stopover to a direct one (Table 4.1). A change in the opposite direction, from direct to stopover in the following year, was observed in a higher proportion during spring migration (three out of 12 individuals; Table 4.1). No individual was observed changing strategy in both directions (Table 4.1).

Table 4.1. Direction and proportion of individuals that changed migratory strategy on each season (Autumn and Spring), from a stopover to direct, direct to stopover or on both directions; n = number of individuals.

Season	n	Median (range) of observations/individual	Strategy change (n)	Direction of change (%)		
				Stop → Direct	Direct → Stop	Both directions
Autumn	16	3 (2-6)	6% (1)	100%	0	0
Spring	12	2 (2-5)	25% (3)	0	100%	0

Along the annual cycle, Icelandic whimbrels showed the highest consistency of timing at spring departure (Figures 4.2 and 4.3, Table 4.2). Despite low *R* values for spring arrival, individuals showed relatively smaller mean individual ranges (Table 4.2) and small absolute interannual differences (Figure 4.3 and Table 4.3) than at autumn migration stages. Such low *R* values result from a relatively

low variance among individuals compared to the variance within (Figure 4.2), which arises from the change in migratory strategies. Spring stopover duration was relatively consistent, with low mean individual range and low absolute interannual differences (Table 4.1, Figure 4.3). During autumn migration, both departure and arrival timings showed similar consistency (Figures 4.2 and 4.3, Table 4.2), as in this season individuals seldom change strategy and almost always perform a direct flight (Table 4.1). However, contrary to autumn departure, autumn arrival absolute interannual difference was not statistically different from laying dates (Table 4.3). Laying date was the least consistent stage of the annual cycle (Figures 4.2 and 4.3, Table 4.2). When considering the absolute interannual difference, we found no overall difference between sexes (Table 4.3), but males showed a lower absolute interannual difference of stopover duration (Figure 4.3, Table 4.2), and a mean individual range in autumn ca. 2.5 days longer than females (Table 4.2).

Table 4.2. Repeatability (*R*) with 95% confidence intervals (CI) of timing of annual events and spring stopover duration, for all individuals (a) and by sex (b and c). Sample size is the number of individuals (n). Also shown is the mean individual range (± se), in days. "Spring arrival (stopover)" represent the arrivals excluding direct flights.

			Repeatability		mean individual
	Stage	n	*R*	CI	range ± se
(a) All					
	Laying	97	0.11	0 - 0.25	10.0 ± 0.77
	Autumn departure	16	0.28	0 - 0.57	9.1 ± 1.65
	Autumn arrival	16	0.26	0 - 0.55	9.3 ± 1.68
	Spring departure	12	0.76	0.42 - 0.91	3.6 ± 0.72
	Stopover duration	11	0.27	0 - 0.68	3.0 ± 0.84
	Spring arrival	12	0.23	0 - 0.60	5.3 ± 1.44
	Spring arrival (stopover)	11	0.48	0 - 0.78	3.0 ± 0.74
(b) Females					
	Laying	42	0.18	0 - 0.40	9.1 ± 1.23
	Autumn departure	7	0.40	0 - 0.76	7.7 ± 2.45
	Autumn arrival	7	0.38	0 - 0.79	7.7 ± 2.67
	Spring departure	6	0.76	0 - 0.94	4.2 ± 1.25
	Stopover duration	5	0.00	0 - 0.65	4.2 ± 1.39
	Spring arrival	6	0.22	0 - 0.76	4.3 ± 2.09
	Spring arrival (stopover)	5	0.55	0 - 0.93	2.0 ± 1.1
(c) Males					
	Laying	54	0.08	0 - 0.26	10.8 ± 1.00
	Autumn departure	9	0.02	0 - 0.39	10.2 ± 2.28
	Autumn arrival	9	0.00	0 - 0.40	10.4 ± 2.19
	Spring departure	6	0.70	0 - 0.92	3.0 ± 0.78
	Stopover duration	6	0.52	0 - 0.86	2.0 ± 0.93
	Spring arrival	6	0.06	0 - 0.55	6.3 ± 2.09
	Spring arrival (stopover)	6	0.00	0 - 0.55	3.8 ± 0.95

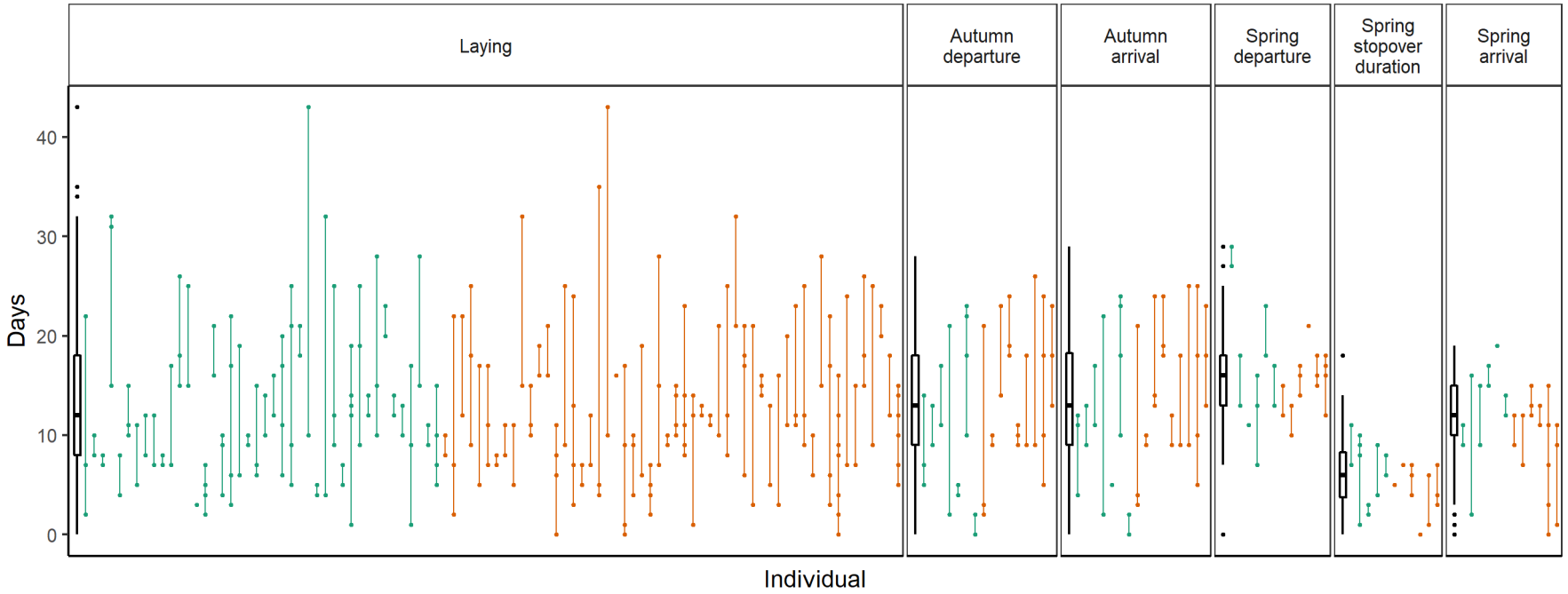

Figure 4.2. Population and individual interannual variation at each stage of the annual cycle for female (green) and male (orange) Icelandic whimbrels. Population data are summarized by the boxplot on the left of each panel (showing the median and 25 and 75% quartiles, whiskers extending up to 1.5 times the inter quartile range from the median and points beyond that are individually marked) and aims to serve as a reference to visually compare individual variation. Each data point shows the timing or duration of the event in a given year and all observations of the same individual are linked with a vertical line; dates were standardized by subtracting the minimum value observed for each stage at the population level. Note that at spring departure one individual left the wintering area considerably early (shown as an outlier), creating and apparent large variation at this stage if only the boxplot (population) is considered; the same individual then performed the longest stopover recorded (upper outlier). Unfortunately, we do not have repeated tracks of this individual to explore consistency in these stages, as it did not return to the breeding sites after the geolocator was replaced.

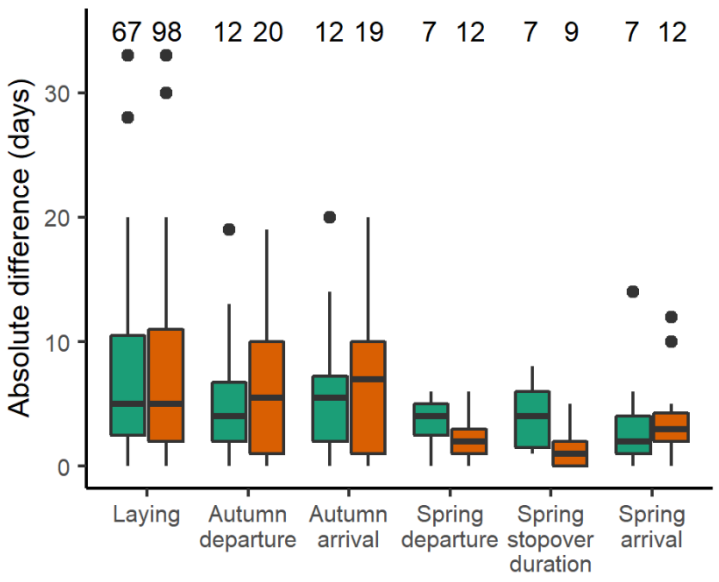

Figure 4.3. Absolute interannual difference in timing for each annual stage, grouped by sex (females in green, males in orange); boxes show the median and 25 and 75% quartiles, whiskers extend up to 1.5 times the inter quartile range from the median and points beyond that are individually marked; the number above each boxplot shows the sample size.

Table 4.3. Results of the general linear model testing the effects of stage and sex on absolute interannual differences; estimates for stages are in relation to laying and for sex it is of male in relation to female.

	Estimate	SE	*t*	*p*
Intercept	1.996	0.045	44.31	**< 0.001**
Autumn departure	-0.276	0.130	-2.12	**0.034**
Autumn arrival	-0.177	0.125	-1.42	0.156
Spring departure	-0.723	0.205	-3.53	**< 0.001**
Spring arrival	-0.684	0.201	-3.40	**0.001**
Spring stopover duration	-0.610	0.194	-3.14	**0.002**
Sex	-0.023	0.059	-0.39	0.700
Autumn departure * Sex	0.256	0.160	1.60	0.109
Autumn arrival * Sex	0.186	0.156	1.20	0.231
Spring departure * Sex	-0.516	0.289	-1.79	0.074
Spring arrival * Sex	0.117	0.250	0.47	0.638
Spring stopover duration * Sex	-0.996	0.341	-2.92	**0.003**

Discussion

By tracking individuals over multiple years and over a considerable part of their lifespan, it is possible to quantify relevant levels of individual consistency or flexibility regarding the phenology of important events during the annual cycle. Both consistency and flexibility can be advantageous depending on the life history of each species (Vardanis et al., 2016), and can be essential to understand the capacity and rate of population responses to changing environments (Gill et al., 2014). The arrival

dates of Icelandic whimbrels in spring have been stable over the past 30 years (Figure 4.1; Gunnarsson and Tómasson, 2011), despite a spring advancement of temperatures that drives resources for waders locally (Alves et al., 2019). At the individual level, we show that Icelandic whimbrels were more consistent in timing of spring than autumn migration, and most consistent at departure from the wintering sites. Timing of laying was the stage of the annual cycle that varied the most and no overall significant difference between sexes was observed, except for males lower absolute interannual difference of stopover duration.

During autumn migration, a lower consistency in timing was observed compared to spring (Tables 4.2 and 4.3, Figures 4.2 and 4.3) and the values at arrival mirror the ones at departure because in nearly all occasions individuals flew directly from Iceland to the wintering sites (Table 4.1; Carneiro et al. 2019). On the other side of the Atlantic, Hudsonian whimbrels showed the same general pattern, as inter-individual variation was greater at autumn departure and arrival dates, than at spring departure and arrival dates (Johnson et al., 2016). Given the expected stable conditions in the wintering area, one could anticipate repeatability to be high during autumn migration (Nussey et al., 2005). In fact, despite a lower consistency in relation to spring, Icelandic whimbrels are still reasonably consistent in autumn migration timings, with a median individual departure range of 9 days and median absolute interannual difference of 5 days, which are in line, or even lower than those observed on other long distance migratory birds (median range of departure of ca. 15 days in individual continental black-tailed godwits *L. l. limosa*, Verhoeven et al., 2019; median absolute interannual difference of ca. 4, 5 and 6 days in bar-tailed godwits *L. lapponica,* marbled godwits *L. fedoa* and red-backed shrikes *Lanius collurio*, respectively, Conklin et al,. 2013, Pedersen et al., 2018, Ruthrauff et al., 2019; mean absolute interannual difference of 12.9 in great reed warblers *Acrocephalus arundinaceus*, Hasselquist et al., 2017). The observed variation in departure dates from Iceland is likely explained by the prior variation in laying dates and breeding success, since successful breeders tend to depart later (pers. obs.). The mean individual range recorded for males (ca. 2.5 days larger than females; Table 4.2) is likely due to their longer attendance of broods.

The relative low repeatability of laying date (Table 4.2, Figures 4.2 and 4.3) may be partially explained by the variation in arrival dates into the breeding sites and partner arrival timing and return. Nevertheless, under a scenario of arctic amplification and spring advancement (Alves et al., 2019; Gill et al., 2014; Høye et al., 2007; Serreze et al., 2009), flexibility on laying dates might be beneficial, allowing individuals to track the local conditions and breed successfully. But the potential advancement of laying might be constrained by previous annual events. While spring arrival dates showed some variability (mean individual range at arrival: 5.3 ± 1.4 days), it was mostly due to variation in migratory strategy (Table 4.1), with the occurrence of a stopover augmenting variation on arrival date after a consistent departure from the wintering sites (mean individual range at departure: 3.6 ± 0.7 days). When considering only the spring arrival of individuals that had a stopover (which is the common strategy), we find higher consistency of arrival dates (mean individual range at arrival: 3.0 ± 0.7 days; Table 4.2). Furthermore, stopover duration also shows considerable

consistency. Hence, individuals tend to be consistent throughout spring migration, starting at departure, which might limit how much laying dates can vary after arrival. If individuals would advance the departure date from the wintering sites, the capacity of tracking the advancement of resource availability in the breeding sites would be higher. However, climatic conditions in the wintering areas seem to be more stable than at the breeding sites (Høye et al., 2007; Serreze et al., 2009; Cohen et al., 2014), and thus unlikely to trigger individual responses at a sufficient rate that allows individuals to track the changes at the breeding sites. In fact, over the last 30 years the population of Icelandic whimbrels showed a stable spring arrival date (Figure 4.1), despite the increasing temperatures in the breeding grounds (Alves et al., 2019; Gunnarsson and Tómasson, 2011).

Populations can change migration timing through transgenerational variation in phenology (Gill et al., 2014). Such a mechanism was identified in Icelandic black-tailed godwits (*L. l. islandica*), that have advanced their arrival date into Iceland and tracked the advancement of spring onset (Gill et al., 2014). Similar to whimbrels, individual godwits are consistent in their timing of spring arrival, but recruits tend to migrate earlier and drive the population timing (Gill et al., 2014). The lack of an advancement in whimbrels population arrival dates into Iceland, together with individual consistency, suggests none, or little, transgenerational changes of migration timing. While black-tailed godwits spend the winter in the temperate region, at a maximum of ca. 3000 km from Iceland (Alves et al., 2012), Icelandic whimbrels migrate longer distances to winter in the tropical or subtropical region, ca. 6000 km from the breeding sites (Carneiro et al., 2019; Gunnarsson and Guðmundsson, 2016). By wintering closer to Iceland (Alves et al., 2013), godwits might adjust arrival dates to the local environment (Alves et al., 2012), lay as soon as conditions are adequate and produce young early in the season, that are more likely to recruit and ultimately drive population changes (Alves et al., 2019). Whimbrels, on the other hand, by wintering further and likely with no cue of the environmental conditions in Iceland, might have narrowed the variation in timing of departure to a later date than godwits and other waders breeding in Iceland, which in turn reduces the variation at spring arrival, the time between arrival and laying and, consequently, laying dates, limiting the possibilities for transgenerational changes. The arrival date into the breeding sites can vary considerably with spring migratory strategy, with individuals arriving earlier after a direct strategy consequently having a longer period in Iceland before breeding and be more likely to track the advancement of spring onset. However, a direct strategy in spring is uncommon, and although our data on its variation is limited, no individual changed from a stopover to a direct strategy, suggesting that individuals might not track the advancement of spring onset through a change in migratory strategy.

Whimbrels show no advancement of arrival dates into Iceland while spring onset is advancing (Figure 4.1; Alves et al., 2019; Gunnarsson and Tómasson, 2011), but there is no indication of a population decline (Skarphéðinsson et al., 2016). In Iceland, whimbrels are one of the latest waders to arrive and have a relatively short breeding period when compared to other species breeding in the same area (Gunnarsson, unpubl. data). The period length of available minimum resources for breeding is unknown, but if it is wider than that required for successful breeding by whimbrels, it could be that

they have been reproducing within that window even while the environmental conditions are advancing. However, under continuous advancement of spring conditions, consistency might prevent individuals from responding to changes when breeding and resource time windows mismatch. At such a hypothetical point one might observe the recruits performing with a different phenology and allow the population to respond to environmental changes, similarly to Icelandic black-tailed godwits. While monitoring population size, it is thus important to acquire knowledge on resource dynamics at the breeding areas (e.g. does the peak abundance of a given resource influence chick growth and survival?), and on the ontogeny of migration and associated timing (e.g. does hatching date affect the migration timing of recruits?). Links between resources and ontogeny will allow understanding how migratory schedules are defined and forecast population-level responses of long-distance migrants to environmental change.

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CHAPTER 5

CATCHING UP WHEN STOPPED: CAN STATIONARY PERIODS BUFFER TIMING DELAYS ON A LONG-DISTANCE MIGRANT?

Previous photo by Tómas G. Gunnarsson.
Icelandic whimbrel landing, Iceland, 23 July 2019.
After chicks hatch, whimbrels tend to perch on high structures more often.

CATCHING UP WHEN STOPPED: CAN STATIONARY PERIODS BUFFER TIMING DELAYS ON A LONG-DISTANCE MIGRANT?

Abstract

Timing can be crucial in order to animals maximize their fitness, but timing of each annual stage can depend on conditions experienced in previous ones. For species with extreme long-distance migrations, it could be expected that carry-over effects associated with delayed completion of tasks (e.g. migration) would be common. However, strong selection in early life may truncate inter individual variation, which associated to a counter-intuitively conservative annual cycle, may allow those effects to be dissipated throughout the year, or not to arise. In species with moderate life-histories but that express some extreme traits, individual variation might be larger, creating an opportunity to understand possible bottlenecks at different annual stages and their implications on population dynamics. Here we take advantage of a population that encompass those characteristics, the Icelandic whimbrel, and use full annual cycle individual level data to investigate correlations between annual stages, duration of stationary periods, and their fitness consequences.

Contrary to species with extreme long-distance migrations, Icelandic whimbrels show a domino effect from autumn migration departure to the following laying date, despite an apparent attempt to compensate for delays during stationary periods. Such a domino effect has the potential to affect breeding output, as fledging success declines with laying date. However, the cumulative time saved at each stationary period seems enough to avoid interannual effects between breeding seasons. These findings suggest that selection pressure and/or the ability to dissipate carry-over effects may vary along a range of migratory distances, where selection during early life and/or on timing of events might be weaker in species migrating shorter distances.

Introduction

Millions of animals migrate between breeding and wintering areas twice a year, often travelling long distances to exploit seasonal resource peaks (Newton 2007, Somveille et al. 2015). Arriving within the optimal schedule to meet those peaks is crucial for individuals to maximise their fitness (McNamara et al. 1998, Kokko 1999, Thomas et al. 2001). A well-established example is the exploitation of food resources during the breeding season, when a mismatch between breeding onset and food can depress breeding success (Visser et al. 1998, Both and Visser 2001). However, arriving too early can also have negative consequences (McNamara et al. 1998, Lerche-Jørgensen et al. 2018), for example if environmental conditions early in the season are more variable and mortality increases (e.g. cold spells; Vepsäläinen 1969, Marcström et al. 1979). Additionally, as each stage is part of the annual (and life) cycle of each individual, the timing of one stage can depend on the timing of the previous one, which can in turn also vary with earlier events, in a series of timing correlations,

creating a ‘domino effect’. While a domino effect may be expected and difficult to overcome during sequential movement stages (e.g. departure and arrival dates), during stationary periods (e.g. migratory stopover) individuals might have the opportunity to adjust their schedule, thus compensate for delays and perform the following stage on time (Conklin and Battley 2012, Senner et al. 2014, Briedis et al. 2018). For example, great snipes *Gallinago media* tend to spend shorter periods in the wintering areas after a late arrival, and individuals that depart later in spring migration have shorter stopover durations during their return to the breeding sites (Lindström et al. 2016).

Carry-over effects arise when “an individual’s previous history and experience explains their current performance in a given situation” (O’Connor et al. 2014). Hence, aspects regarding habitat quality, social status and breeding effort, for example, can lead to variation on individuals’ body condition and schedule, and carry-over across stages during the annual cycle (Norris et al. 2004, Rockwell et al. 2012, Catry et al. 2013). For example, if a delayed migrant does not “correct” its timing during pre-nuptial phases, negative carry-over effects might arise through a late arrival at the breeding sites with associated negative consequences for breeding success (Bêty et al. 2004, van Wijk et al. 2017). Given the importance of the phenology of specific annual events, timing is likely to be a common driver of carry-over effects, and a trait that can be reversed (Senner et al. 2015).

Extreme life-histories often amaze us, and very long bird migrations are good examples. After breeding in Alaska, bar-tailed godwits *Limosa lapponia baueri* cover 11700 km in a non-stop flight to New Zealand and return in spring migration undertaking two flights, of 10000 and 7000 km with a stopover at the Yellow Sea (Battley et al. 2012). Given such an extreme annual routine, it could be expected that carry-over effects would arise, as delays may be hard to recover when undertaking extremely long journeys, but this is not the case (Conklin and Battley 2012). Conklin and colleagues (2017) reviewed evidence on life-history traits for a set of 19 species of migratory waders performing non-stop flights of 5000 – 11700 km. They proposed that these birds have a counter-intuitively conservative annual cycle that minimises risks and allows the dissipation of carry-over effects, and that early life selection pressure eliminates low-performing individuals from the population. The main focus of that review was the Alaska-breeding bar-tailed godwit, for which the full annual cycle has been studied in detail (e.g. Battley 2006, Gill et al. 2009, Conklin et al. 2010, 2013, Battley et al. 2012, Conklin and Battley 2012). While this prototypical species shows reduced individual variation (Conklin et al. 2013), other long-distance migrants performing shorter migratory flights and with a less extreme life-history, may manifest larger individual variation and thus present an opportunity to further understand possible bottlenecks at different phases (e.g. breeding, migration, wintering), and their implications on population dynamics (Norris 2005).

Icelandic whimbrel *Numenius phaeopus islandicus*’ life-history provides a valuable system to investigate how inter-seasonal carry-over effects arise through phenology, are dissipated, and may influence individual breeding success. This subspecies breeds mainly in Iceland and in autumn it migrates in a single flight, typically of 6000 km, to spend the winter in West Africa. During spring, it

either performs a direct flight (direct strategy), or, more commonly, a 5000 km flight to a stopover site in Britain and Ireland, followed by another flight of 1500 km to Iceland (stopover strategy; Carneiro et al. 2019). These flights lay on the lower end of 'extremeness' as considered by Conklin et al. (2017), allowing a broader insight into the gradient of effects that extreme migration can have at the individual level. The occurrence of a maximum of two stationary periods outside the breeding areas – wintering and one stopover during spring migration – provides a simple system and a rare opportunity to investigate time compensation within the annual cycle. Using full annual cycle data at the individual level, we investigate correlations between annual stages (arrival and departure dates during migration and laying date) and duration of stationary periods (wintering, stopover, arrival-lay gap), and their fitness consequences in Icelandic whimbrels. By establishing how long-distance migrants may deal with delays, we will improve our understanding on their capacity to respond to environmental change.

Methods

Data collection

During the breeding seasons of 2012 to 2017, in the southern lowlands of Iceland (63.8°N; 20.2°W), 188 whimbrels were caught on the nest using a nest trap (Moudry TR60; www.moudry.cz). The wing length (maximum chord, to the nearest mm) and body mass (to the nearest g) of each individual was recorded and, from 14 birds, a blood sample was collected and stored in 96% ethanol. One hundred and two whimbrels were individually marked with colour rings (from 2015 to 2017) and to 86 a geolocator was attached to a flag (Fig. 5.1A). The geolocator was usually retrieved in the following year and often replaced, using the same catching and deployment techniques. In total, 133 devices were deployed (model Intigeo-W65A9RJ, 0.65g, from 2012 to 2014, n = 23, and Intigeo-C65, 1.0g, in the following years, n = 110; Migrate Technology Ltd; whimbrel average (± se) body mass: 432.7 ± 3.4g). Sixty-two geolocators were possible to retrieve (45%), from 37 individuals, despite the overall return rates being higher (Table 5.1). In order to assess the effect of the geolocator on return rates, chi-square tests were used to investigate differences in the returning proportions, between birds marked with colour rings only and those also carrying a geolocator. The sex of each individual was determined using biometrics following Katrínardóttir et al. (2013; n = 19), molecularly (as in Katrínardóttir et al. 2013; n = 14) or through behavioural observation (copulating position, assuming that males were on top; n = 4).

Upon finding the nests, eggs were floated in order to estimate laying date and predict hatching date (Liebezeit et al. 2007). Nests were then monitored until hatching and for those that hatched, the laying date was back-calculated (and the previous estimate replaced) assuming an incubation period of 25 days after the last laid egg (mean ± se: 24.8 ± 0.2 days, n = 24 nests found when laying and for which hatching date was also recorded). In most cases, hatchlings were ringed upon hatching or in following visits as the broods were regularly monitored until fledging (27 days of age) and fledging

success recorded (i.e. successful, if one or more chicks fledged; or unsuccessful, if no chicks fledged).

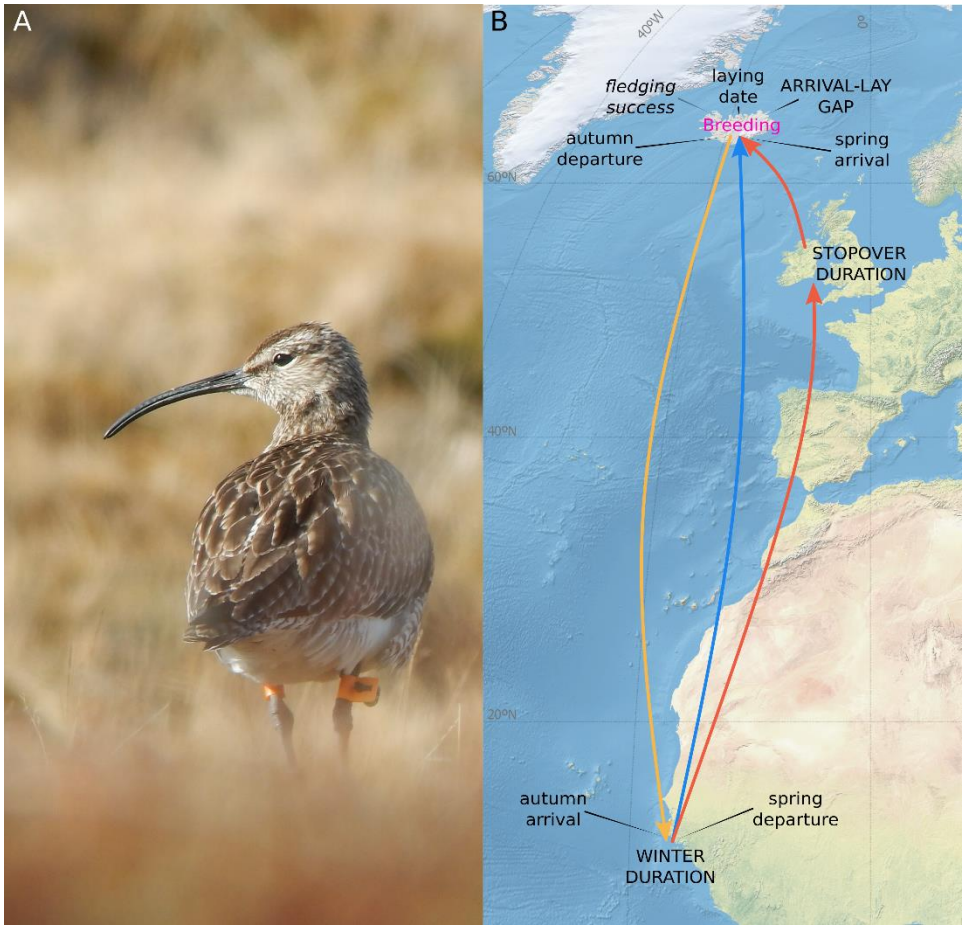

Figure 5.1. (A) Icelandic whimbrel wearing a leg flag with a geolocator. The device is on the opposite side of the orange flag, while the end of the cable tie used to attach it is clearly visible. (B) Schematic representation of the main migratory strategies of Icelandic whimbrels (direct spring migration in blue and stopover in red) and the variables considered in this study. Stationary periods are shown in capital letters, annual stages in lowercase and fledging success in italics.

Migration data from geolocators were analysed as described in Carneiro et al. (2019). All dates were converted to ordinal day of the year. The following migratory stages were extracted: autumn and spring migration departure and arrival, and spring stopover arrival and departure (Fig. 5.1B). The wintering and stopover durations were calculated as the number or days between arrival and departure and the arrival-lay gap as the number of days between spring arrival and laying date (Fig. 5.1B). Total stationary duration was calculated as the sum of the three aforementioned stationary periods (i.e. wintering + stopover + arrival-lay gap). In the case of three individuals that stopped twice during spring migration, stopover duration was considered the sum of both stopovers. The relative timing of individuals at each annual stage was calculated in relation to the population mean for that stage, across years. The timings of one individual (YR-YLf) were considered outliers at certain stages

of the annual cycle and the data of this individual was therefore excluded from the analyses but is shown in the plots.

Statistical analysis

We used linear mixed models (LMM) to test the effect of previous annual cycle stages, spring migratory strategy (direct or stopover) and sex of individuals on the subsequent stages and interannual effects between breeding seasons. Fledging success, sex and their interaction were used as predictors of differences in autumn departure date from Iceland. To test for differences in winter departure date and winter duration, winter arrival date, fledging success, sex, migratory strategy and the interaction of migratory strategy with sex were used as predictor variables. The date of winter departure, migratory strategy, sex and interactions of migratory strategy with winter departure and with sex were used to test for differences in spring arrival date. To test for differences in spring stopover duration, winter departure date and sex were used as explanatory variables. To test for differences in laying date and in arrival-lay gap, arrival date into Iceland and migratory strategy were used as predictors. To test for interannual effects of one breeding season on the timing of the following breeding season, laying date was used as the response variable and autumn departure date, previous fledging success and their interaction as explanatory variables. Autumn departure date, previous fledging success, their interaction, sex and migratory strategy were used as predictor variables to test for differences in total stationary duration. In all LMMs individual identity and year were used as random effects (although year estimate collapsed to zero in some cases; see results). Finally, a generalized linear mixed model (with binomial error distribution) was used to evaluate the effect of laying date on fledging success, with individual identity as random effect. Given the limited sample size, the interaction terms were removed when not significant and final models contained all fixed effects (even when not significant). Models with non-significant interaction terms are shown in supplementary material (Tables A5.1.1 and A5.1.2). Function ‘lmer’ in R with restricted maximum likelihood and ‘glmer’ were used (package ‘lme4’; Bates et al. 2015) and statistical significance of fixed effects were calculated with package ‘lmerTest’ (Kuznetsova et al. 2016). Data were analysed in R (R Core Team 2018) and results are shown as mean ± se, unless otherwise stated.

Results

Between 2012 and 2018, 68 autumn migrations (plus the departure date of one case in which the geolocator stopped functioning soon after) and 56 spring migrations of 37 individuals were recorded. The return rate of individuals carrying geolocators varied annually between 60% and 100%, although retrieval rates were usually lower (25% to 100%) as nests were often predated before recapturing the birds (Table 5.1). Geolocators did not seem to have a detrimental effect, as the return rate of birds carrying a geolocator was not statistically different from those carrying colour rings only (Table 5.1).

Table 5.1. Annual return rate of individuals marked in the previous year, carrying a geolocator or colour rings only. Some returning individuals with geolocators were not recaptured, hence the retrieval rate for this group is also shown. Chi-square tests were used to compare the return rates between groups in three years of the study. n: individuals marked in the previous year;

Year	Geolocators			Colour rings		Chi-square	
	return rate (%)	retrieval rate (%)	n	return rate (%)	n	χ^2	*p*
2013	70.0	50.0	10				
2014	100.0	100.0[A]	3				
2015	70.0	50.0	10				
2016	60.0	40.0[B]	30	55.6	36	0.01	0.91
2017	72.5	45.0[B]	40	65.0	40	0.23	0.63
2018	60.0	25.0[C]	40	73.1	26	0.68	0.41

[A] plus one deployed two seasons before; [B] plus two deployed two seasons before; [C] plus three deployed two seasons before and one three seasons before.

Most individuals wintered between Senegal and Sierra Leone (89%; but mainly in Guinea-Bissau and Guinea-Conakri, 81%) and the remaining between Morocco and Mauritania. We found no effect of sex or fledging success on the date of departure in autumn migration, but a significant interaction (Table 5.2A), in which successful males departed later than successful females and unsuccessful breeders (Fig. 5.2A). The timing of autumn arrival was highly correlated to departure (Pearson r = 0.99; n = 67, p < 0.001), as could be expected given that Icelandic whimbrels tend to fly non-stop from Iceland to the wintering sites (Alves et al. 2016, Carneiro et al. 2019b; although one individual made a stopover of 4 days in autumn). The date of departure from the wintering sites was positively affected by the previous autumn arrival, individuals that performed a direct flight in spring migration tented to depart later, while previous fledging success and sex had no effect (Table 5.2B, Fig. 5.2B). Sex and fledging success also had no effect on the duration of the wintering period, but this period decreased significantly with autumn arrival date and was shorter for individuals that performed a stopover strategy in spring (Table 5.2C, Fig. 5.2C). The spring arrival date into Iceland was positively affected by the date of departure from the wintering site and migratory strategy, with birds that flew direct arriving earlier (Table 5.2D, Fig. 5.2D). Sex had no effect on spring arrival date, but its interaction with strategy did, as males that performed a stopover strategy arrived earlier than females (Table 5.2D, Fig. 5.2D). Spring stopover duration was negatively affected by departure date from the wintering site and was shorter for males than females (Table 5.2E, Fig. 5.2E). Laying date had a positive relationship with arrival date into Iceland and did not vary with spring migratory strategy or sex (Table 5.2F, Fig. 5.2F). Although not statistically significant (Table 5.2G), the arrival-lay gap showed a negative tendency with spring arrival date (Fig. 5.2G), but no influence of migratory strategy or sex (Table 5.2G). Fledging success varied significantly with laying date, being higher early in the season (Table 5.2H, Fig. 5.2H).

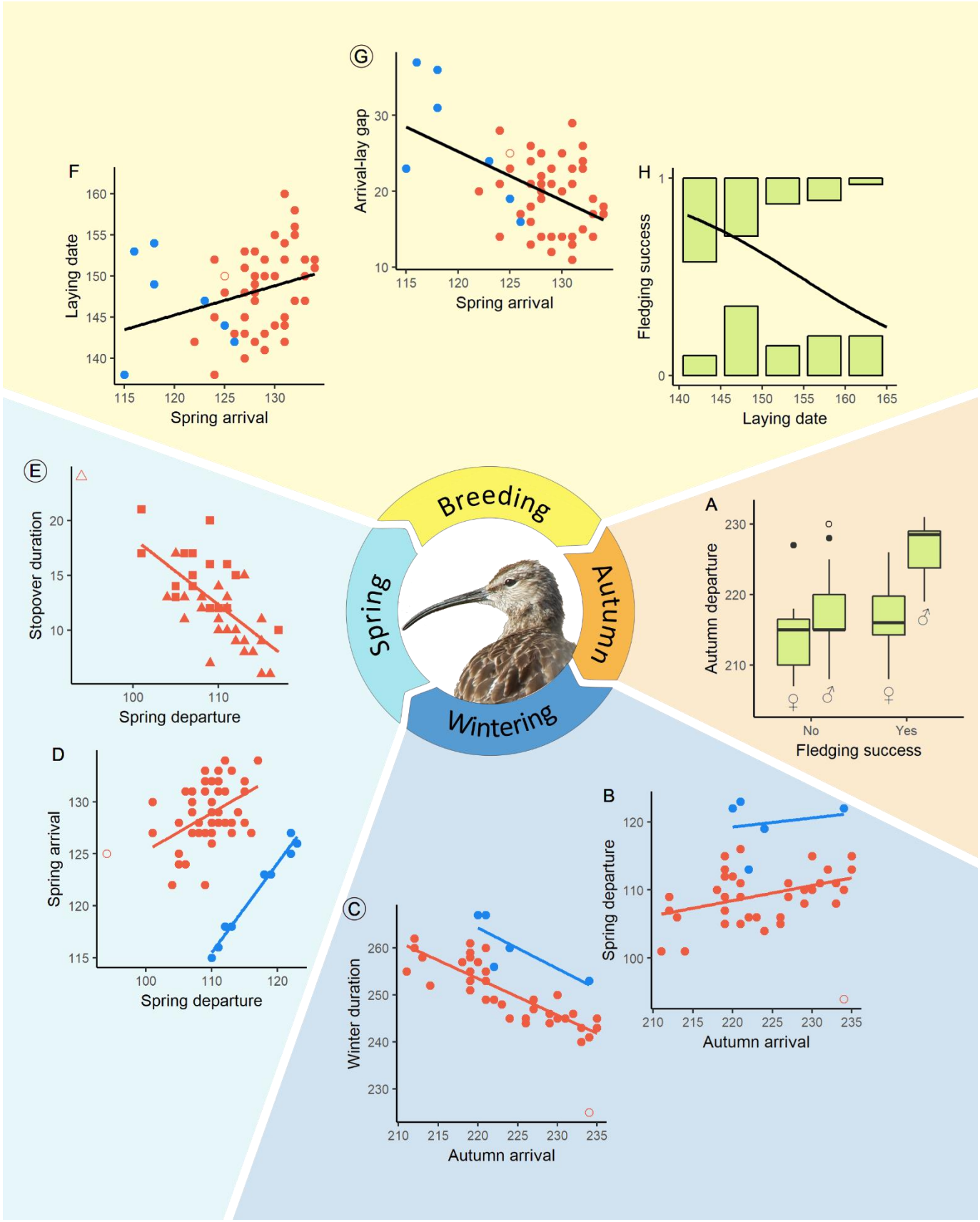

Figure 5.2. Intra and inter-seasonal relationships throughout Icelandic whimbrel's annual cycle. The size of each annual period (breeding, autumn migration, wintering and spring migration) in the circle is not scaled to real relative time; dates of stages (arrival and departure on migration and laying) are represented in the ordinal day of the year; stationary periods (wintering and stopover duration and the arrival-laying gap) are measured in days; colours inside scatterplots represent spring migratory strategy (red: stopover; blue: direct) and symbols represent sex (squares: females; triangles: males) where sex differences are significant; the empty symbol on each plot represents individual YR-YLf which is not included in the analysis (see methods for details). Circled letters highlight relationships between an annual stage and a stationary period.

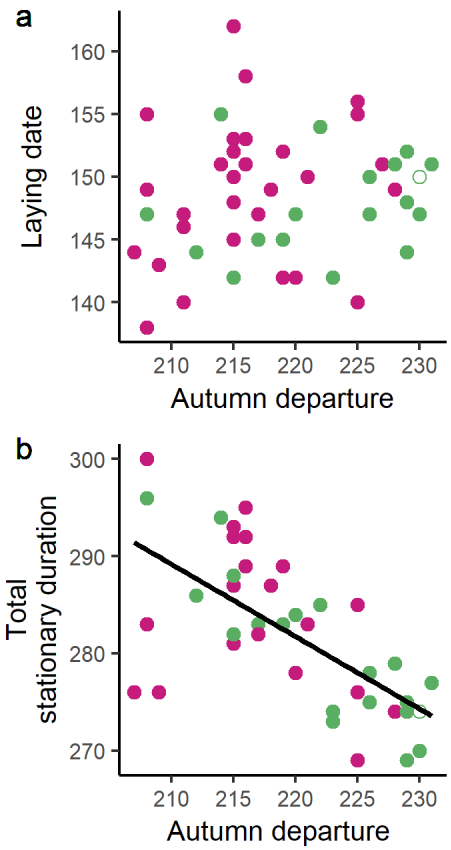

Figure 5.3. Variation of (a) laying date and (b) total stationary duration in function of the autumn departure date in the previous year, coloured by previous fledging success (unsuccessful: pink; successful: green). Numbers represent the ordinal day of the year, except for stationary duration, which is represented in total days; the empty circle represents individual YR-YLf and is not included in the analysis (see methods for details).

There was no apparent effect of fledging success or autumn departure date on the following year's laying date (Table 5.3a, Fig. 5.3a). Autumn departure date had a negative effect on total stationary duration, but fledging success, sex of the individual, migratory strategy and the interaction of autumn departure date and fledging success had no effect (Table 5.3b, Fig. 5.3b). Nevertheless, and although the relative timing of individuals at each stage clearly changed throughout the year, early departure in autumn tends to link with early laying date in the following breeding season, despite such link not being apparent at spring arrival date (Fig. 5.4).

Discussion

In extreme long-distance migrants (such as the Alaska-breeding bar-tailed godwit), carry-over effects are rare, likely due to a strong early-life selection and a conservative annual cycle that allow their dissipation (Conklin et al. 2017). However, species exhibiting moderate migration (i.e. shorter migratory flights), while showing a considerably conservative annual cycle (e.g. few migratory flights, short-breeding period), can provide enough individual variation and thus a unique opportunity in which to explore carry-over effects. Using full annual cycle data of individual Icelandic whimbrels (which spend ca. three months in the breeding area, complete the annual migratory movements in three flights and show sufficient individual variation; Carneiro et al. 2019a, b), we show a domino effect arising from autumn migration departure date up to the following laying date, despite an apparent attempt to compensate for delays during stationary periods. Such a domino effect has the potential to affect breeding output, since fledging success declines with laying date. However, we found no direct relationship between the preceding fledging success or autumn departure date on subsequent laying date, because the sum of time spent at stationary periods since autumn departure until the following laying date allows to compensate for delays between breeding seasons.

Table 5.2. Model results testing the effect of several variables (second column) on each annual stage, stationary period or fledging success (first column). Estimates for sex are of male in relation to female; and strategy is for stopover in relation to direct. Letters match those in plots of Figure 5.2.

	Linear Mixed Models								
	Fixed effects						Random effects		
		Estimate	SE	df	*t*	*p*		Variance	SD
Autumn departure	Intercept	213.81	2.02	10.40	105.64	**<0.001**	individual	6.32	2.51
n = 52	Fledging success	3.39	2.08	46.62	1.63	0.110	year	5.43	2.33
A	Sex	3.26	1.94	33.14	1.68	0.103	Residual	16.84	4.10
	Fledging succ. * Sex	5.66	2.73	43.88	2.07	**0.044**			
Spring departure	Intercept	73.26	19.27	22.79	3.80	**0.001**	individual	9.13	3.02
n = 42	Autumn arrival	0.19	0.09	23.16	2.18	**0.040**	year	0.00	0.00
B	Fledging success	1.75	1.12	29.80	1.56	0.129	Residual	3.35	1.83
	Sex	1.63	1.52	33.63	1.07	0.291			
	Strategy	-8.50	1.66	33.37	-5.13	**<0.001**			
Winter duration	Intercept	438.26	19.27	22.79	22.75	**<0.001**	individual	9.13	3.02
n = 42	Autumn arrival	-0.81	0.09	23.16	-9.11	**<0.001**	year	0.00	0.00
C	Fledging success	1.75	1.12	29.80	1.56	0.129	Residual	3.35	1.83
	Sex	1.63	1.52	33.63	1.07	0.291			
	Strategy	-8.50	1.66	33.37	-5.13	**<0.001**			
Spring arrival	Intercept	58.99	9.71	48.06	6.07	**<0.001**	individual	0.93	0.96
n = 55	Spring departure	0.54	0.08	47.26	6.52	**<0.001**	year	0.00	0.00
D	Strategy	11.73	1.04	50.24	11.28	**<0.001**	Residual	4.54	2.13
	Sex	-2.61	0.70	27.91	-3.71	**<0.001**			
Stopover duration	Intercept	67.87	10.42	35.84	6.52	**<0.001**	individual	1.27	1.13
n = 46	Spring departure	-0.61	0.10	36.41	-5.07	**<0.001**	year	0.29	0.54
E	Sex	-2.91	0.76	19.34	-3.85	**0.001**	Residual	3.35	1.83
Laying date	Intercept	74.26	25.04	44.65	2.97	**0.005**	individual	5.60	2.37
n = 55	Spring arrival	0.60	0.20	43.84	2.94	**0.005**	year	10.54	3.25
F	Strategy	-3.60	2.41	43.14	-1.49	0.143	Residual	13.71	3.70
	Sex	0.75	1.43	31.20	0.52	0.607			
Arrival-lay gap	Intercept	74.26	25.04	44.65	2.97	**0.005**	individual	5.60	2.37
n = 55	Spring arrival	-0.40	0.20	43.84	-1.96	0.057	year	10.54	3.25
G	Strategy	-3.60	2.41	43.14	-1.49	0.143	Residual	13.71	3.70
	Sex	0.75	1.43	31.20	0.52	0.607			
	Generalized Linear Mixed Model								
	Fixed effects						Random effect		
Fledging success	Intercept	0.79	0.47		1.67	0.094	individual	2.80	1.67
n = 101	Laying date[1]	-1.12	0.51		-2.19	**0.029**	year	0.10	0.31
H									

[1]variable was rescaled

Table 5.3. Model results testing the effect of (a) previous autumn departure date, fledging success and their interaction on laying date; and of (b) previous autumn departure date, fledging success, sex, migratory strategy and interaction of autumn departure and fledging success on pre-breeding stationary period. Estimates for sex are of male in relation to female; and strategy is for stopover in relation to direct. Letters match those in plots of Figure 5.3.

	Linear Mixed Models								
	Fixed effects						Random effects		
		Estimate	SE	df	*t*	*p*		Variance	SD
Laying date	Intercept	121.49	25.76	46.88	4.72	**<0.001**	individual	8.45	2.91
n = 52	Autumn departure	0.12	0.12	47.01	1.05	0.301	year	2.64	1.62
a	Fledging success year X-1	-1.21	1.51	48.15	-0.80	0.429	Residual	14.19	3.77
Total stationary duration	Intercept	456.01	40.59	36.48	11.24	**<0.001**	individual	4.94	2.22
	Autumn departure	-0.79	0.19	36.36	-4.16	**<0.001**	year	11.60	3.41
n = 42	Fledging success year X-1	0.88	2.15	35.79	0.41	0.686	Residual	25.36	5.04
b	Sex	-0.99	2.42	29.81	-0.41	0.687			
	Strategy	-1.16	2.92	32.68	-0.40	0.694			

Timing compensation in the wintering site

In whimbrels, males tend to care longer for the brood than females (BWPi 2006), which likely explains why successful males departed later than females in autumn migration (Fig. 5.2A). This contrasts with the longer distance migratory Hudsonian godwits *Limosa haemastica*, in which no effect of breeding success was observed in the relative timing of autumn departure (Senner et al. 2014). Also in contrast with Hudsonian godwits, bar-tailed godwits (Conklin and Battley 2012), great snipes (Lindström et al. 2016) and collared flycatchers *Ficedula albicolis* (Briedis et al. 2018), is the relationship between autumn arrival and spring departure, in which late arriving Icelandic whimbrels depart later from the wintering sites (Fig. 5.2B), whilst in the other species spring departure date is independent from autumn arrival. This occurred despite the apparent attempt of Icelandic whimbrels to compensate for a delay in winter, indicated by the negative relationship between autumn arrival and winter duration, which was shorter for individuals arriving later (Fig. 5.2C). Similarly to Icelandic whimbrels, European nightjars *Caprimulgus europaeus* also showed a decrease of winter duration with autumn arrival date and a positive relationship between autumn arrival and spring departure dates (Norevik et al. 2017).

A late autumn arrival and shorter period in the wintering areas might entail costs. The main and likely most energetically expensive tasks at those sites are the complete feather moult and fuelling for migration. While in bar-tailed godwits wing moult is influenced by autumn arrival date (Conklin and Battley 2012), in Icelandic whimbrels this is unlikely, because complete moult requires only ca. 90 - 120 days (Ginn and Melville 1983), and the shortest winter duration recorded was much longer (240 days). Even considering a period of 50 days for migratory fuelling (Carneiro et al. 2019b), it seems unlikely that a delay in autumn arrival has a considerable effect in the duration of those tasks. A later arrival could, however, mean that those individuals may only be able to occupy lower quality territories and therefore potentially take longer to gather resources for moulting and fuelling. Still,

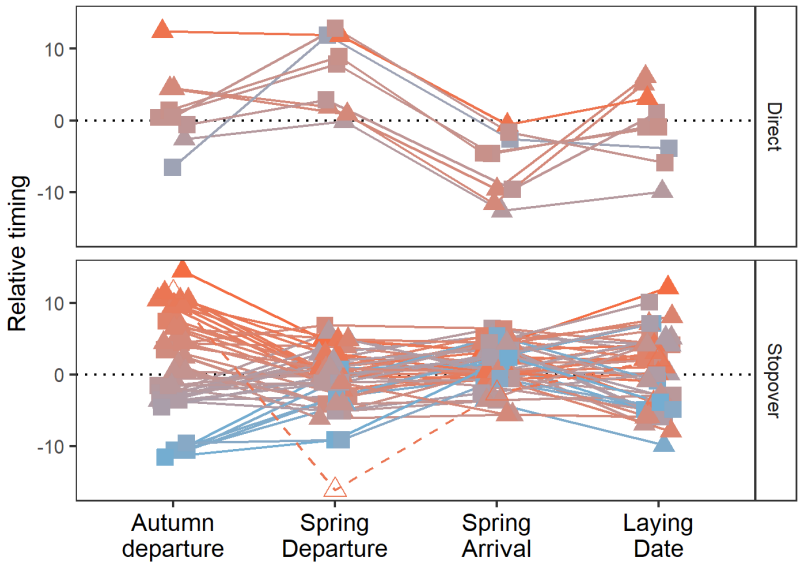

Figure 5.4. Relative timing (to the mean) of each individual at each annual stage grouped by spring migratory strategy (upper panel: direct; lower panel: stopover). Colder colours represent earlier individuals at departure from Iceland, while warmer represent later ones; females are represented by squares, males by triangles and the empty triangle is individual YR-YLf, which is not included in the analysis (see methods for details).

even considering such potential limitation, it seems unreasonable that during the relatively long wintering period whimbrels would be time restricted in completing those tasks. Nevertheless, the positive relationship between autumn arrival and spring departure, suggests that there may be constraints limiting a full compensation during the longest stationary period.

Timing compensation at spring stopover

As expected, departure and arrival dates in spring migration are correlated for individuals performing direct flights between the wintering and breeding sites. However, such relationship was also observed when individuals performed a stopover (Fig. 5.2D). Stopover duration decreased with increasing spring departure date (Fig. 5.2E), suggesting another attempt to compensate for delays. Comparable behaviour at stopover was recorded in white storks *Ciconia ciconia* (Rotics et al. 2018), great snipes (Lindström et al. 2016) and European nightjars (Norevik et al. 2017). In the latter case, there was also a positive relationship between arrival and departure from the stopover sites (Norevik et al. 2017), indicating insufficient timing compensation similarly to Icelandic whimbrels that undertook a stopover strategy.

Although no information is available regarding individual body condition at stopover arrival, it is plausible that whimbrels need to store fuel for the following flight (of ca. 1500 km). Given limitations in fuel deposition rates (Lindström 2003), there is likely a minimum number of days required to fuel, which could explain why late arriving individuals may not be able to depart earlier. On the other hand, spending time at the stopover site might be an investment on body condition, if at the stopover areas individuals attain a higher rate of resource accumulation than at the breeding areas. This may be beneficial upon arrival to Iceland (Alerstam 2006), as it might allow time saving by starting energy-demanding activities as quickly as possible (Davidson and Evans 1988, Gudmundsson et al. 1991). Additionally, stopover may occur for individuals to assess the weather conditions in the breeding

grounds prior to arrival (Chapter 6), and maybe favourable conditions are more likely later in the season, shortening the stopover duration of late arriving individuals.

Timing compensation in the breeding site

During the last stationary period prior to breeding – the arrival-lay gap – the pattern is similar to that of the previous two stationary periods of the annual cycle. Icelandic whimbrels laying date varies positively with spring arrival date (Fig. 5.2F), despite the negative relationship of spring arrival date and arrival-lay gap (Fig. 5.2G). Early arrival at the breeding sites is often linked to early laying (e.g. Hoopoe *Upupa epops* van Wijk et al. 2017; American redstart *Setophaga ruticilla*, Norris et al. 2004; tree swallow *Tachycineta bicolor*, Gow et al. 2019; and fork-tailed flycatchers *Tyrannus savanna*, Bejarano and Jahn 2018), which is likely due to the probability of higher breeding success for early breeders (Perrins 1970, Drent 2006, Morrison et al. 2019). Indeed, fledging success decreases with laying date in Icelandic whimbrels (Fig. 5.2H). It seems therefore important for individuals to avoid delays in arrival at the breeding sites, in order to lay when chances of fledging young are higher. However, due to the observed domino effect, arrival date in spring depends on the previous spring departure, which in turn depends on the previous autumn arrival date.

Other carry-over effects

Although carry-over effects operating through timing of events are the main focus of the present analysis, individual fitness can also be influenced by other factors. For example wintering site quality can influence spring departure date, as in American redstarts *Setophaga ruticilla* (Marra et al. 1998); the arrival date into the breeding sites, as in black-tailed godwits *Limosa limosa* (Alves et al. 2013); the laying date, as in collared flycatchers (Briedis et al. 2018); and the body condition in the breeding sites, as is the case of house martins *Delichon urbicum* (López-Calderón et al. 2017). In Icelandic whimbrels, despite individuals achieving distinct energetic balance at different wintering sites, neither laying date or egg volume varied with wintering area (Chapter 3). Hence, we observe potential carry-over effects between consecutive stages due to delays, while wintering habitat quality has no apparent effect on breeding timing or investment in this system.

Dissipating carry-over effects along the annual and life cycles

It seems plausible that Icelandic whimbrels try to compensate for delays at stationary periods in order to perform on time in the following stage or later in the year. This is in agreement with recent research on the full annual cycle of other long-distance migrants (Senner et al. 2014, Lindström et al. 2016, Norevik et al. 2017, Briedis et al. 2018), suggesting it might be a common mechanism in these systems. In the case of extreme long-distance migratory waders, a timing resetting mechanism at stationary periods might help to explain the counter-intuitive lack of inter seasonal carry-over effects on these species (Conklin et al. 2017). Icelandic whimbrels lay at the lower end of extreme long-distance migrants proposed by Conklin and colleagues (2017), and contrary to species on the opposite side of the spectrum – e.g. Hudsonian and bar-tailed godwits (Conklin and Battley 2012,

Senner et al. 2014) – timing compensation at each stationary period seems to be insufficient (Fig. 5.2), with less capacity to dissipate carry-over effects. This might indicate a range of selection pressure or ability to dissipate carry-over effects along the range of migratory distance, where selection during early life and on timing of events might be weaker in shorter than longer distance migrants (Conklin et al. 2017). In the case of Icelandic whimbrels, evidence suggests that wind conditions tend to be more favourable during autumn than spring migration (Alves et al. 2016), which may mean a low to moderate selection pressure early in life (i.e. during the first migration) and allow larger individual differences in the population to persist.

While Icelandic whimbrels shown an apparently insufficient timing compensation at each stationary period of the annual cycle, the timing of laying seems to be independent from the previous breeding season, due to a timing compensation during all stationary periods (Table 5.3, Fig. 5.2). Hence, at the annual scale and between breeding seasons carry-over effects (in the form of time) seem to be dissipated. However, early individuals at autumn departure tend to lay early in the following year (Fig. 5.4), suggesting that some interannual effect may be occurring. Given that individual Icelandic whimbrels tend to be consistent on their annual schedules (Carneiro et al. 2019a), they might be limited in the degree of possible time compensation at each stage. Nevertheless, the sum of the (small) variation across several annual stages and stationary periods may allow for individual timing compensation between breeding seasons. For example, if an individual performs earlier at each stage prior to a stationary period by 50% of the mean individual range for that stage (i.e. 4.6 days earlier at autumn arrival, 1.8 at spring departure and 2.6 at spring arrival; Carneiro et al. 2019a), that bird will be able to “save” 6.3 days (3.5, 1.1 and 1.7 days at each stationary period, respectively; values calculated from linear regressions with annual stage as independent and stationary duration as dependent variable) and thus lay earlier comparing to a scenario of no compensation. Such variation in timing of laying is within the mean individual range recorded (10 days; Carneiro et al. 2019a) and can influence the likelihood of fledging young by ca. 16%.

In sum, despite at each stationary period Icelandic whimbrels fail to fully compensate for delays, the cumulative time saved at each seems enough to avoid interannual effects between breeding seasons. Readjusting the schedule at stationary periods is likely to be widespread across migrants and may be more prevalent on long-distance migrants with shorter travelling distances. The increasing volume of individuals tracked throughout the annual cycle across systems varying on migration length, associated to an investigation of inter-seasonal carry-over effects, will further clarify these patterns and processes. Furthermore, conditions at non-breeding areas (wintering and stopover sites) seem particularly important for long-distance migrants to adjust their annual schedule and breed on time, highlighting their importance for these species.

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Appendices

Appendix 5.1

Table A5.1.1. Model results, prior to selection depending on the significance of the interaction terms (see methods), testing the effect of several variables (second column) on each annual stage, stationary period or fledging success (first column). Estimates for sex are of male in relation to female; and strategy is for stopover in relation to direct. Letters match those in plots of Figure 5.2.

	Linear Mixed Models								
	Fixed effects						Random effects		
		Estimate	SE	df	*t*	*p*		Variance	SD
Autumn departure	Intercept	213.81	2.02	10.40	105.64	**<0.001**	individual	6.32	2.51
n = 52	Fledging success	3.39	2.08	46.62	1.63	0.110	year	5.43	2.33
A	Sex	3.26	1.94	33.14	1.68	0.103	Residual	16.84	4.10
	Fledging succ. * Sex	5.66	2.73	43.88	2.07	**0.044**			
Spring departure	Intercept	72.94	19.44	21.97	3.75	**0.001**	individual	9.55	3.09
n = 42	Autumn arrival	0.19	0.09	22.23	2.17	**0.041**	year	0.00	0.00
B	Fledging success	1.75	1.13	28.74	1.54	0.134	Residual	3.37	1.84
	Sex	1.89	4.11	31.88	0.46	0.649			
	Strategy	-8.39	1.86	28.39	-4.52	**<0.001**			
	Sex * Strategy	-0.30	4.16	32.08	-0.07	0.944			
Winter duration	Intercept	437.94	19.44	21.97	22.53	**<0.001**	individual	9.55	3.09
n = 42	Autumn arrival	-0.81	0.09	22.23	-9.01	**<0.001**	year	0.00	0.00
C	Fledging success	1.75	1.13	28.74	1.54	0.134	Residual	3.37	1.84
	Sex	1.89	4.11	31.88	0.46	0.649			
	Strategy	-8.39	1.86	28.39	-4.52	**<0.001**			
	Sex * Strategy	-0.30	4.16	32.08	-0.07	0.944			
Spring arrival	Intercept	18.20	21.85	47.72	0.83	0.409	individual	1.05	1.03
n = 55	Spring departure	0.88	0.18	47.26	4.79	**<0.001**	year	0.00	0.00
D	Strategy	55.90	24.10	48.55	2.32	**0.025**	Residual	4.09	2.02
	Sex	1.19	1.79	48.67	0.66	0.511			
	Spr. departure * Strategy	-0.36	0.21	48.28	-1.76	0.084			
	Sex * Strategy	-4.10	1.91	48.97	-2.14	**0.037**			
Stopover duration	Intercept	67.87	10.42	35.84	6.52	**<0.001**	individual	1.27	1.13
n = 46	Spring departure	-0.61	0.10	36.41	-5.07	**<0.001**	year	0.29	0.54
E	Sex	-2.91	0.76	19.34	-3.85	**0.001**	Residual	3.35	1.83
Laying date	Intercept	74.26	25.04	44.65	2.97	**0.005**	individual	5.60	2.37
n = 55	Spring arrival	0.60	0.20	43.84	2.94	**0.005**	year	10.54	3.25
F	Strategy	-3.60	2.41	43.14	-1.49	0.143	Residual	13.71	3.70
	Sex	0.75	1.43	31.20	0.52	0.607			
Arrival-lay gap	Intercept	74.26	25.04	44.65	2.97	**0.005**	individual	5.60	2.37
n = 55	Spring arrival	-0.40	0.20	43.84	-1.96	0.057	year	10.54	3.25
G	Strategy	-3.60	2.41	43.14	-1.49	0.143	Residual	13.71	3.70
	Sex	0.75	1.43	31.20	0.52	0.607			
	Generalized Linear Mixed Model								
	Fixed effects						Random effect		
Fledging success	Intercept	0.79	0.47		1.67	0.094	individual	2.80	1.67
n = 101	Laying date[1]	-1.12	0.51		-2.19	**0.029**	year	0.10	0.31
H									

[1]variable was rescaled

Table A5.1.2. Model results, prior to selection depending on the significance of the interaction terms (see methods), testing the effect of (a) previous autumn departure date, fledging success and their interaction on laying date; and of (b) previous autumn departure date, fledging success, sex, migratory strategy and interaction of autumn departure and fledging success on pre-breeding stationary period. Estimates for sex are of male in relation to female; and strategy is for stopover in relation to direct. Letters match those in plots of Figure 5.3.

	Linear Mixed Models							
	Fixed effects						Random effects	
		Estimate	SE	df	*t*	*p*	Variance	SD
Laying date	Intercept	108.16	34.66	47.97	3.12	**0.003**	individual	8.68	2.95
n = 52	Autumn departure	0.19	0.16	47.97	1.16	0.251	year	2.60	1.61
a	Fledging success year X-1	26.87	49.02	46.22	0.55	0.586	Residual	14.32	3.79
	Autumn departure * Fledging success year X-1	-0.13	0.22	46.28	-0.57	0.569			
Total stationary duration	Intercept	412.69	50.62	34.57	8.15	**<0.001**	individual	4.43	2.11
	Autumn departure	-0.59	0.23	34.50	-2.51	**0.017**	year	11.57	3.40
n = 42	Fledging success year X-1	90.74	63.41	32.35	1.43	0.162	Residual	24.97	5.00
b	Sex	-0.56	2.40	28.19	-0.23	0.819			
	Strategy	-0.98	2.87	31.91	-0.34	0.735			
	Autumn departure * Fledging success year X-1	-0.41	0.29	32.45	-1.42	0.166			

CHAPTER 6

THE ROLE OF WEATHER AND PHENOLOGY IN DRIVING SPRING MIGRATORY STRATEGIES OF A LONG-DISTANCE MIGRANT

Previous photo by Triin Kaasiku.
Running away, Iceland, 30 June 2019.
Whimbrel chicks blend well into the habitat.

THE ROLE OF WEATHER AND PHENOLOGY IN DRIVING SPRING MIGRATORY STRATEGIES OF A LONG-DISTANCE MIGRANT

Abstract

Migration can represent a significant part of an individual annual cycle and the strategies used to move between the breeding and non-breeding areas vary considerably. Weather conditions are important during migration, particularly wind and temperature, and can play a crucial role in the annual cycle of migratory birds through its influence on subsequent events. When timing is important, for example spring arrival and laying dates, the effects of weather on the previous migration might have important fitness consequences as it can slow down or increase migration speed. During spring, Icelandic whimbrels *Numenius phaeopus islandicus* undertake two main migratory strategies: a direct flight from the wintering to the breeding sites (direct strategy), or, more commonly, two flights with one stopover (stopover strategy). We investigated how wind conditions, temperature and spring departure date may drive individuals to adopt either migratory strategy, and found no differences in wind support during migration, in temperature closer to Iceland or on crosswinds experienced in the region before reaching the main stopover sites. However, departure date from the wintering sites was on average later when individuals performed a direct flight to the breeding areas, and was not explained by wind selectivity over a period of seven days prior to departure. In addition, we explored the variation at the individual level for three birds that changed migratory strategy between years. The variation in all variables for these three individuals reflected the variation observed at the population level. By undertaking a direct strategy, individual whimbrels arrive earlier at the breeding sites, but do not necessarily breed earlier. Hence, it might be advantageous to perform a shorter flight to the stopover area, from where the weather conditions at breeding may be assessed and avoid the risk of stochastic inclement weather prior to breeding.

Introduction

Migration can represent a significant part of an individual annual cycle and the strategies used to move between the breeding and non-breeding areas vary considerably (Newton 2007, Hansson and Åkesson 2014). Animals may take advantage of the flow of the medium where they move (e.g. air or water) to support migration (Chapman et al. 2011) and optimal bird migration theory postulates that energy and time costs should be kept at a minimum (Alerstam and Lindström 1990). Hence, weather conditions are often taken into consideration during migration, particularly wind and temperature, as these parameters have been shown to influence migration at different stages and in different ways (Shamoun-Baranes et al. 2017). During flight, wind can be favourable but also cause birds to extend the length of migration (Gill et al. 2014), drift due to crosswinds (Grönroos et al. 2013, Horton et al. 2016) or even force stops (Shamoun-Baranes et al. 2010, Klaassen et al. 2017). The links between

temperature and migratory flights are less known, but temperature has been shown to influence individuals' flight altitude (Senner et al. 2018). At stationary locations (e.g. during wintering or stopover), individuals can select favourable winds for departure (Schaub et al. 2004, Gill et al. 2014), or depart regardless of wind conditions (Alerstam et al. 2011); and temperature can also influence the decision of when to leave (Berchtold et al. 2017). Weather conditions can therefore play a crucial role on the annual cycle of migratory birds and changes in the atmospheric patterns at a large scale may influence whole populations or species, through costs of energy and time during migration (La Sorte and Fink 2017, La Sorte et al. 2018). Understanding the mechanisms shaping migratory behaviour might thus help predicting how these species will respond to variation in weather patterns.

When the timing of specific annual cycle events is relevant, such as the timing of breeding which influences breeding success (Perrins 1970, Drent 2006), the effect of weather during migration might have important fitness consequences, as it can slow down or increase migration speed (Alerstam and Gudmundsson 1999, Shamoun-Baranes et al. 2010). For example, if an individual encounters unfavourable weather conditions during pre-nuptial migration, it may increase the duration of migration, arrive at the breeding grounds later, reproduce later and thus experience lower breeding success than conspecifics breeding earlier (Drake et al. 2014). It might therefore be expected that these birds will select the best wind support at departure. But if wind conditions at departure are stable, the timing of departure should be independent of it (Weber and Hedenström 2000). In addition, there can be particular risks associated to long flights over unsuitable habitat for landing or foraging, as unfavourable weather conditions encountered *en route* may lead to more energy expenditure and increase the probability of fuel stores depletion before reaching a suitable location and, in extreme conditions, result in mortality (Newton 2006).

Icelandic whimbrels (*Numenius phaeopus islandicus*) typically complete their annual migrations in two or three flights (Alves et al. 2016, Carneiro et al. 2019b). After breeding in Iceland, autumn migration is completed in one flight over open waters to the wintering sites, which are mostly located in West Africa. During spring, however, two main migratory strategies have been identified: a direct strategy, where whimbrels again fly non-stop to Iceland, and a stopover strategy, where individuals travel first to a stopover site (usually in Britain and Ireland) and then fly to the breeding sites (7-17 days later; Carneiro et al. 2019b). Hence, these two strategies differ in the travel duration from the winter sites to Iceland, but also in the timing of arrival at the breeding sites, with direct migrants arriving earlier than those undertaking a stopover strategy (Chapter 5). Overall, in Icelandic whimbrels, there is a sequential relationship between arrival date, laying date and breeding success, in which early arrival tends to be beneficial in terms of breeding success (Chapter 5), although laying date seems to be independent of previous migratory strategy (Chapter 5). Despite this, the stopover strategy is more common, occurring in 80% of the occasions (Carneiro et al. 2019b). Although there is evidence that departure date can influence the spring migration strategy of Icelandic whimbrels (Chapter 5), the role of weather conditions in influencing such strategy remains unstudied.

Here, we explore how wind conditions, temperature and departure date from winter location relate to the spring migratory strategy of Icelandic whimbrels. We envisage three non-mutually exclusive scenarios: whimbrels select the migratory strategy (i) during flight, depending on conditions already experienced *en route* up to the suitable stop-over locations*;* (ii) at departure (or before) given local conditions, or (iii) are forced to stop due to westerlies. In order to assess the first hypothesis, we define a "decision" latitude where birds might change overall direction of migration (and strategy), and test if wind support experienced until crossing this latitude, and if temperature experienced at this latitude, differs between individuals undertaking either strategy. We expect that wind conditions experienced *en route* will be more favourable and/or temperature higher when individuals perform a direct strategy, as the fuel reserves should be higher and temperature can act as a cue that conditions in Iceland are likely to be favourable upon arrival. To investigate if strategy is selected at departure, we test the role of departure date from the wintering sites, and the influence of wind support at this stage. To assess if birds make a stopover by drifting due to eastward winds, we compare the zonal (longitudinal) wind conditions experienced between strategies when individuals approach the main stopover region and expect these winds to be stronger when a stopover strategy is undertaken. Additionally, using three repeatedly tracked birds that changed migratory strategy over the years, we explore how individual level variation compares to population level variation.

Methods

From 2012 to 2017, 86 adult whimbrels were caught on the nest, in the southern lowlands of Iceland (63.8°N; 20.2°W), using a spring trap (Moudry TR60; www.moudry.cz). Each bird was fitted a combination of colour rings and a geolocator attached to a leg flag (model Intigeo-W65A9RJ from 2012 to 2014 and Intigeo-C65 in following years; Migrate Technology Ltd). Individuals were caught using the same technique one or more years later in order to retrieve and replace the devices, for repeated tracking over the years. We deployed a total of 133 geolocators, and retrieved 62, from 37 individuals, despite the return rate to the breeding areas being higher (Table 5.1). One device was damaged and contained no data, another stopped recording shortly after departure from Iceland, and a third in mid-winter.

In order to estimate geographical locations, light data recorded by the geolocators was analysed as described in Carneiro et al. (2019b). Given that these data only allow a minimum temporal resolution of 12h (two locations per day), we used geolocator recorded data on temperature, conductivity and wet contacts (recorded every four hours) to refine timings of departure and arrival (Battley & Conklin, 2017; see details in Carneiro et al. 2019b). Stopover and winter locations were defined, for each individual and tracked year, as the average of all locations during each period. We assumed the last geographical position on stopover (i.e. departure location) to be the one temporally closest to the time defined by the temperature, conductivity and wet contacts; and departure location from the wintering site was assumed to be the wintering location. For the latter, an exception was made in five cases, in which a movement southward was observed at spring departure. We considered this

unlikely and due to geolocation precision errors through shading, assumed migration from the first position on the track northwards. The location of arrival into Iceland was assumed to be the breeding region (63.8°N, 20.2°W).

Although most migrations were performed in one flight or two flights with one stopover, in three cases individuals made two stopovers. In order to simplify the analysis, these were excluded. Additionally, one individual with a very early departure from the wintering site, in relation to conspecifics, was also excluded from the analyses.

Temperature and wind data

Temperature and wind data were retrieved from the National Centres for Environmental Prediction (NCEP; Kanamitsu et al. 2002), using the R package 'RNCEP' (Kemp et al. 2012a). Although bird migration can occur at higher altitudes (e.g. Alerstam and Gudmundsson 1999), whimbrel flight altitude during migration is unlikely to be higher than 1500 m a.s.l. (Alves et al. 2016, unpublished data). Hence, data was retrieved for each location, from a grid of 2.5x2.5º, at the air pressure of 1000, 925 and 850 hPa, representing altitudes of 111, 762 and 1457 m above sea level, respectively.

Based on visual inspection of whimbrel tracks (Carneiro et al. 2019b), we defined a "decision latitude" at 42°N, where individuals might change the overall migration direction and strategy, and a "decision window" between 37 and 50°N, i.e. the region before the main stopover locations in Britain and Ireland, where individuals might be influenced and pushed east by zonal winds to make a stopover, as westerlies prevail in this region. Additionally, given the subjectivity of the assumptions above and the error associated with geolocator positional data (ca. 200km; Phillips et al. 2004, Shaffer et al. 2005, Fudickar et al. 2012), we also considered a "decision" latitude at 37°N and 47°N, representing ca. 10% of the average distance between wintering and breeding sites, assuming a great circle route, south (before) and north (after) of 42°N, respectively. The locations and time when crossing 37°N, 42°N and 47°N were interpolated linearly, assuming constant ground speed.

For all individuals, each location attained during migration, and wintering site, was annotated with the zonal (u) and meridional (v) wind components (Kemp et al. 2012a). In order to investigate wind support during migratory flight, we calculated the flow assistance (FA) as the tailwind component (Kemp et al. 2012b) and the air-to-ground speed ratio (AGR; Alerstam 1979, Gill et al. 2014). The distance between positions was calculated as the great circle distance using the function 'distCosine' of the R package 'geosphere' (Hijmans 2016). Ground speed was calculated as the speed between consecutive positions during migratory flights, and air speed as the difference of ground speed and the FA component. Hence, when AGR < 1 the individual is experiencing wind support, while AGR >1 indicates that wind is an impediment to movement. The AGR value at wintering departure for one individual was an outlier (14.05). Since this could have been due to an erroneous location, either at departure or the following one, both locations and associated wind components were removed from further analysis.

Statistical analysis

We built a generalised linear model (GLM; family binomial) in order to test whether migratory strategy varies with mean AGR until 42°N, air temperature at 42°N and departure date from the wintering sites, for each air pressure (1000, 925 and 850 hPa). In addition, we built similar models considering migration until latitudes 37°N and 47°N.

In order to test for the influence of wind while crossing the region between 37 and 50°N, we restricted the data to locations within that window and built a GLM (family binomial) with migratory strategy as independent variable and the zonal wind component as explanatory variable, which represents east/west winds. As above, this model was performed for each air pressure (1000, 925 and 850 hPa). Although variables such as sex, year and individual may influence spring migration strategy, these variables were not included in these models which given sample size limitations (i.e. observations biased towards stopover strategy, which is far more common; Carneiro et al. 2019b) prevented models to converge or led to overdispersion.

In order to assess if wind support at the wintering site can influence departure date, we retrieved the u and v wind components, from NCEP (Kanamitsu et al. 2002, Kemp et al. 2012a), at the same altitudes as above, for the date and location of departure and for each of the previous seven days (at the same time of the day as the day of departure). Then, we calculated the AGR and performed a Kruskal-Wallis test to examine for differences between days.

Among the individuals with repeated tracks, only three changed migratory strategy. Using these data, we further explored individual variation between strategies using the same variables as above. Data were analysed in software R (R Core Team 2018) and results are reported as mean ± se, unless otherwise stated.

Results

We compared nine direct to 43 stopover spring migration strategies, performed by 34 individuals (Fig. 6.1). Stopover sites were located along the Portuguese continental Atlantic coast (n = 2), northwest of France (n = 3), and Ireland and NW United Kingdom (n = 38; Fig. 6.1).

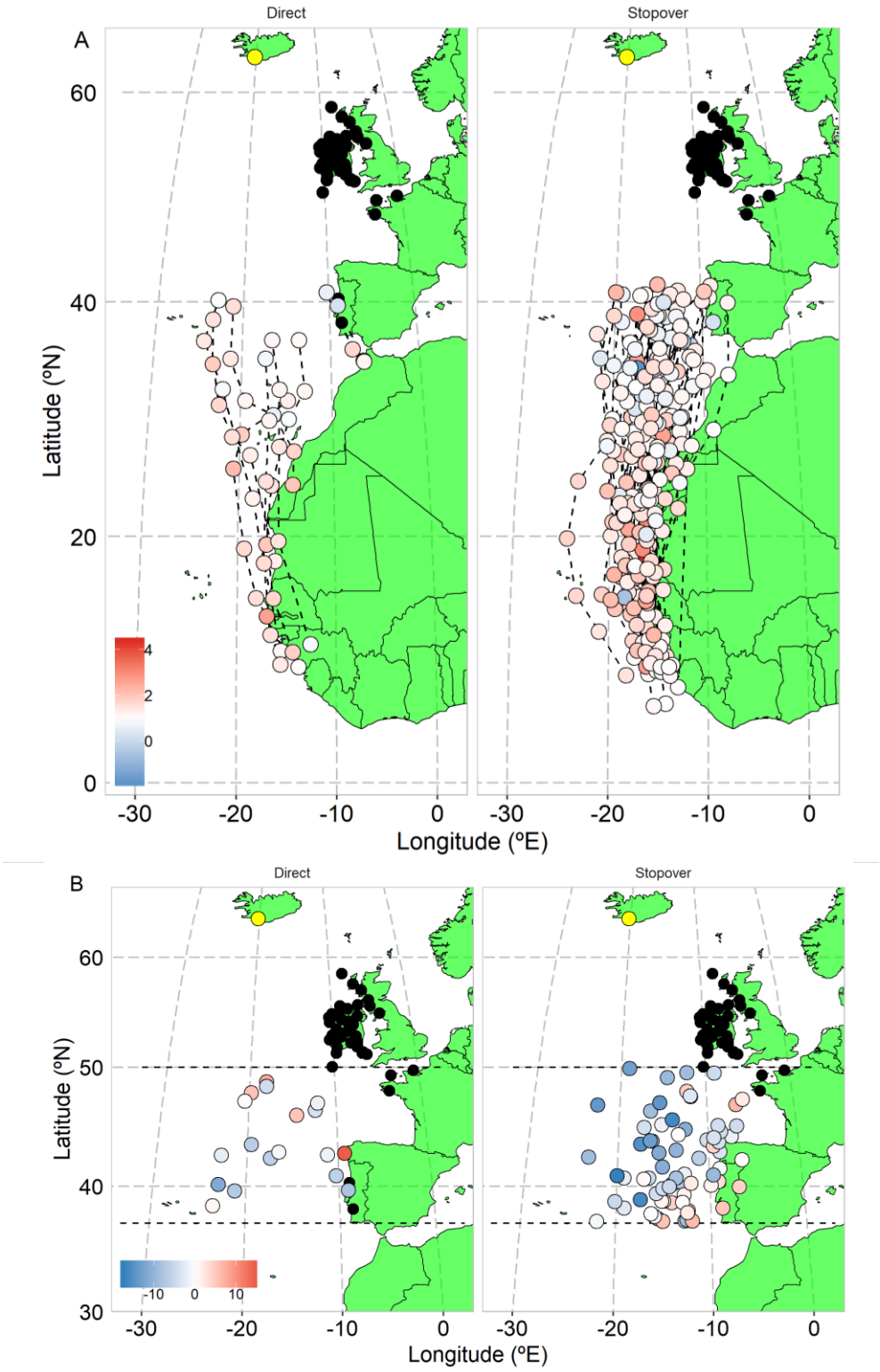

Figure 6.1. (A) Spring migration locations recorded with geolocators up to latitude 42°N, coloured by air-to-ground speed ratio (at 1000 hPa); blue represents wind support (values below one), whereas red represents wind impediment in the direction of movement (values above one). (B) Locations during spring migration between latitudes 37 and 50°N, coloured by zonal wind (u, at 1000 hPa), where blue (negative) values represent westward winds and red (positive) values eastward winds. Circles depict stopover (black) and breeding (yellow) locations. Left panels show locations of individual whimbrels undertaking a direct strategy and right panels of a stopover strategy.

Table 6.1. Generalized linear models testing potential drivers of spring migratory strategy: (A) individual mean air-to-ground speed ratio (AGR) experienced up to crossing 42°N, air temperature at 42°N and departure date from the wintering sites; and (B) zonal wind (east/westward) experienced between 37 and 50°N, for all locations recorded across individuals.

	Air preassure (hPa)		Estimate	SE	*z*	*p*
Migratory strategy	1000	Intercept	43.10	14.68	2.94	**0.003**
n = 52		Mean AGR	1.92	2.13	0.90	0.368
A		Air temperature	0.17	0.34	0.48	0.629
		Departure date	-0.41	0.13	-3.17	**0.002**
	925	Intercept	46.47	14.68	3.17	**0.002**
		Mean AGR	2.04	2.29	0.89	0.374
		Air temperature	0.04	0.22	0.17	0.869
		Departure date	-0.42	0.13	-3.13	**0.002**
	850	Intercept	46.93	14.77	3.18	**0.001**
		Mean AGR	0.62	2.47	0.25	0.802
		Air temperature	-0.07	0.15	-0.50	0.618
		Departure date	-0.40	0.13	-3.00	**0.003**
Migratory strategy	1000	Intercept	1.19	0.28	4.22	**<0.001**
n = 90		U wind	-0.07	0.05	-1.55	0.122
B						
	925	Intercept	1.22	0.27	4.45	**<0.001**
		U wind	-0.07	0.04	-1.71	0.088
	850	Intercept	1.32	0.27	4.91	**<0.001**
		U wind	-0.07	0.04	-1.68	0.092

For the air pressures considered, the mean air-to-ground speed ratio until 42°N and air temperature at that latitude did not differ for whimbrels undertaking either strategy (Table 6.1A, Figs. 6.1A and 6.2A-B). But departure date from the wintering sites did, with birds that departed later tending to undertake a direct flight (mean = 27 April ± 1.7 days, n = 9, and mean = 20 April ± 0.5 days, n = 43, for direct and stopover strategies, respectively; Table 6.1A, Fig. 6.2C). When considering a "decision" latitude at 37°N or at 47°N, the results were similar (Table A6.1.1, Fig. A6.1.1).

The zonal wind component when crossing the region from latitude 37°N to 50°N was not different between migratory strategies at any air pressure considered (Table 6.1B, Figs. 6.1B and 6.2D), and was predominantly westward (e.g. for 1000 hPa: mean = -1.49 ± 1.52, n = 18, and -4.03 ± 0.71, n = 72, for direct and stopover strategies, respectively).

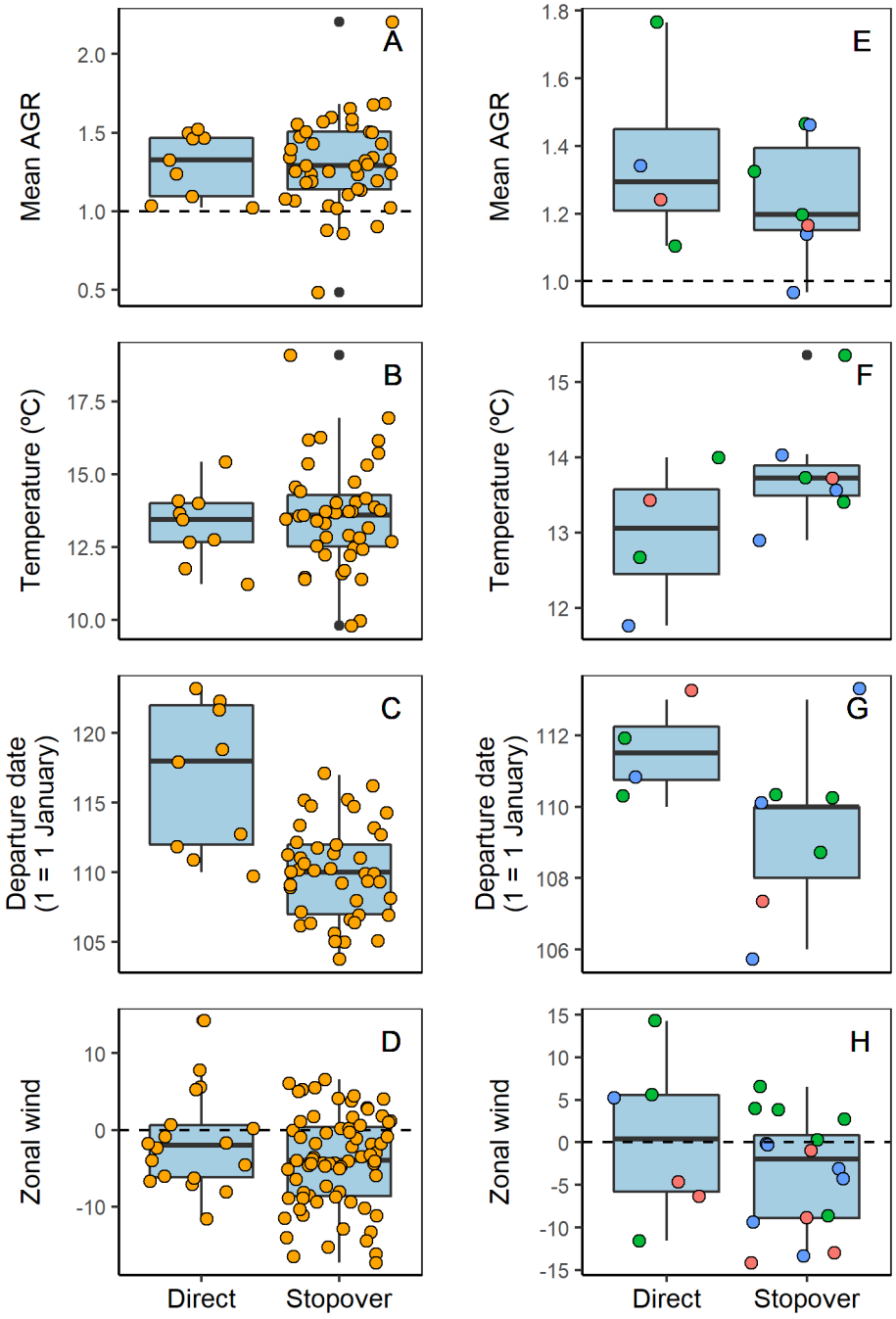

Figure 6.2. Variation in potential drivers of spring migratory strategy (direct vs stopover) of Icelandic whimbrels at the population (left column; A-D) and individual levels (right column, E-H). The three individuals that changed migratory strategy in spring between years (right column) are coded by colour. (A and E) Mean individual air-to-ground speed ratio (AGR) from departure up to latitude 42°N (values below one represent wind support, while values above one mean impediment in the direction of movement); (B and F) Air temperature experience by each individual at latitude 42°N; (C and G) Departure date from the wintering site; (D and H) Zonal wind (u) component, between 37 and 50°N. All data presented here refers to air pressure 1000 hPa (i.e. 111 m a. s. l.). Boxplots show the median and 25 and 75% quartiles, whiskers extending up to 1.5 times the inter quartile range from the median and points beyond that are individually marked in black.

Wind support at departure (measured as AGR at an air pressure of 1000 hPa) did not differ between the day of departure and the previous seven days (Kruskal-Wallis χ^2= 2.325, df = 7, p = 0.940; Fig. 6.3). Similar results were obtained for air pressures of 925 hPa (Kruskal-Wallis χ^2= 2.014, df = 7, p = 0.959; Fig. A6.1.2) and 850 hPa (Kruskal-Wallis χ^2= 2.887, df = 7, p = 0.895; Fig. A6.1.2).

Three individuals changed migratory strategy, from direct to stopover (Fig. A6.1.3). The overall pattern at 1000 hPa, of mean AGR, departure date and zonal winds was similar to that recorded at the population level (Figs. 6.2E, G and H). However, temperature at 42°N tended to be higher when individuals made a stopover (Figure 6.2F), but the difference between mean values was only of 0.8°C (13.0 ± 0.49, n = 4 and 13.8 ± 0.29, n = 7, for direct and stopover strategies, respectively).

Discussion

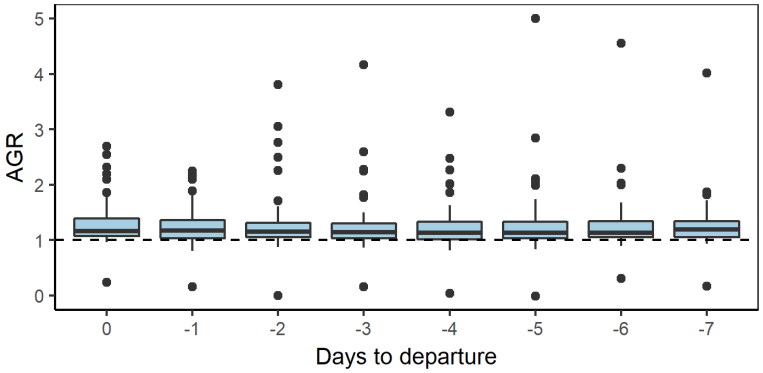

Figure 6.3. Air-to-ground speed ratio (AGR) at the time of departure (0) and at each 24h intervals prior to that time, for the air pressure of 1000 hPa (i.e. 111m a. s. l.; values below one represent wind support, while values above one mean impediment in the direction of movement). Boxplots show the median and 25 and 75% quartiles, whiskers extending up to 1.5 times the inter quartile range from the median and points beyond that are individually marked.

During spring migration, Icelandic whimbrels undertake two main migratory strategies: a direct flight from the wintering to the breeding sites (direct strategy), or two flights with one stopover (stopover strategy). We investigated how wind conditions, temperature and spring departure date may drive individuals to adopt each migratory strategy, and found no differences in wind support during migration, on temperature closer to Iceland or on crosswinds experienced in the region before reaching the main stopover sites. However, departure date from the wintering sites was on average later for individuals performing a direct flight to the breeding areas, and was not explained by wind selectivity over a period of seven days prior to departure.

Neither wind support during flight nor the temperature experienced closer to Iceland differed between individuals undertaking each migratory strategy, suggesting that such decision is unlikely to be made during flight, or at least not due to these parameters. Similarly, whimbrels were not forced to stop by eastward winds, as no differences on these were found when crossing the region before the main stopover areas and both strategies tended to experience more westward winds. While other long distance migratory waders may capitalise on wind drift during migratory flight and modify their route accordingly (Gill et al. 2014), whimbrel spring migration strategy seems to be unaffected by wind conditions, within the considered flight altitudes and range of wind speeds recorded in this study.

Departure date can also be influenced by weather conditions, as birds often select favourable winds (Ma et al. 2011, Gill et al. 2014). Long-distance migrating bar-tailed godwits (*Limosa lapponica baueri*) generally experience favourable conditions during the departure period from the wintering sites, creating few opportunities for wind assistance selectivity. Yet, most off-schedule individuals tend to depart when wind assistance is maximised (Conklin and Battley 2011). In the case of Icelandic whimbrels, wind conditions at departure were not different from those recorded during the previous week, and were predominantly unfavourable, suggesting none to low selectivity for wind assistance. However, other factors may also influence the departure date of individuals, such as the amount of fuel reserves (Sjöberg et al. 2015), temperature (Berchtold et al. 2017) and joining a flock of departing conspecifics, which may be important in orientation during flight (Alerstam et al. 1990).

Given the apparent stable conditions at departure and the importance of time in this system (Chapter 5), the lack of wind selectivity is not surprising and could explain the direct strategy when individuals depart later. For Icelandic whimbrels, breeding success tends to decline with laying date (Chapter 3), and laying date varies with arrival date (Chapter 5). By undertaking a direct strategy, individuals arrive earlier to the breeding sites, in relation to those undertaking a stopover (Chapter 5), which may allow to compensate for a delay. However, and despite the overall positive arrival-laying relationship, the laying date does not seem to differ between strategies (Chapter 5), suggesting that a direct flight may in fact not always translate into higher breeding success.

If a direct strategy is not clearly advantageous and conditions during spring migration flight are not different between strategies (until the same stage of migration), then why is the latter more prevalent across the population? The main stopover sites are located in Britain and Ireland, which are relatively close to the breeding sites, in Iceland. Hence, individuals might be able to assess the weather conditions at breeding locations during stopover, and adjust arrival date into Iceland when those are favourable (Gunnarsson and Tómasson 2011, Alves et al. 2012), thus avoiding the risk of stochastic inclement weather prior to breeding (Newton 2006). In fact, the temperature at departure from the stopover locations tends to be positively correlated to the temperature in the breeding areas, suggesting that if whimbrels depart when weather is good locally at the stopover site, they are likely to find favourable conditions upon arrival in Iceland (Spearman $r = 0.445$, $S = 735$, $p = 0.003$; Fig. 6.4). Additionally, or alternatively, a stopover might serve to improve body condition at a faster rate than in Iceland and give individuals an advantage upon arrival at the breeding sites (Alerstam 2006).

At the individual level, for the three birds that changed migratory strategy, the variation in all variables reflects the patterns also observed at the population level. However, the variation is smaller, as would be expected because Icelandic whimbrels tend to be consistent in their timing, particularly at spring departure (Carneiro et al. 2019a). The differences in departure date between strategies at the individual level, given such small variation in this annual stage overall, support the role of departure date in the migratory strategy used. Additionally, the fact that individuals only changed from a direct to a stopover strategy, further suggests an individual refinement of strategies (Fig A6.1.4). Given that

there appears to be no clear advantage from a direct flight, a shorter flight to a stopover site might involve fewer risks due to unpredicted weather conditions at arrival and fuel depletion, and still allow a timely arrival at the breeding sites.

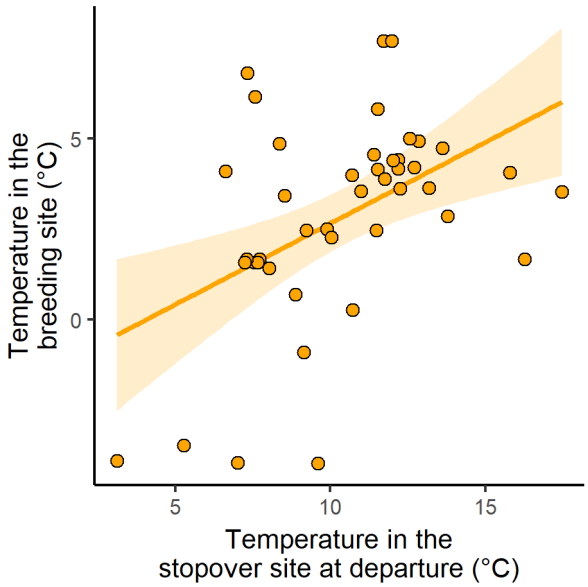

Figure 6.4. Relationship between the temperature at the time of departure from the stopover site and the temperature in Iceland at the same time; a linear regression is represented with 95% confidence intervals.

Our analyses show that wind conditions encountered during migration are not the main driver of different spring migratory strategies in Icelandic whimbrels, but these results need to be considered with caution. First, in our statistical models, individual identity was not included as a random effect (see methods), which may influence (at least some of) the variation explained by the other variables. Nevertheless, individuals can perform both strategies and vary in departure time in the same way as the population (Fig. 6.2), therefore the effect of pseudo-replication is likely low. Second, there is a considerable error associated to locations from geolocators (Phillips et al. 2004, Shaffer et al. 2005, Fudickar et al. 2012), which may influence the direction and speed calculated, and consequently the FA and AGR. However, given the amount of locations during migration available in the dataset, if wind conditions had an important effect, it should still be detected. Third, we used FA as the tailwind component, which is a simple method with few assumptions and ignores perpendicular wind flow in relation to the direction of the birds movement (Kemp et al. 2012b), simplifying a likely more complex behaviour. Lastly, as the flight altitude of the individuals tracked here is unknown, we assumed whimbrels fly at constant altitudes which restricts the natural dynamics of flight.

Weather conditions experienced at departure or during flight seem to be irrelevant for the selection of a direct or stopover strategy by Icelandic whimbrels during spring, but strategy varies with departure date. Whether departure date is a cause or a consequence of migratory strategy, remains to be investigated. Records of whimbrels body condition prior to departure from the wintering grounds associated to departure date and migratory strategy used, will likely help to clarify this question.

Predicted changes in climate include changes in patterns of atmospheric circulation (IPCC 2013), which have the potential to influence avian migration at a large scale (La Sorte and Fink 2017, La Sorte et al. 2018). Although under the contemporary scenario the selection of spring migratory strategy (direct vs. stopover) by Icelandic whimbrels is not determined by wind conditions, the

situation may change in a future environment with different atmospheric circulation. An alteration in wind support may affect time and energetic costs (La Sorte et al. 2018). If energetic costs increase, the importance of quality and location of fuelling sites along the migration route should increase too, as more resources will be required to cover the same distance. Hence, for those species performing long flights over unsuitable habitat even migration routes may require adjustment in order to accommodate suitable stopover locations.

Acknowledgements

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Appendices

Appendix 6.1

Table A6.1.1. Generalized linear models testing potential drivers of spring migratory strategy: individual mean air-to-ground ratio (AGR), air temperature and departure date from the wintering sites, at three 1000 hPa, 925 hPa and 850 hPa, representing 111, 762 and 1457 m above sea level, respectively, and until reaching latitude 37, 42 and 47°N. Sample size = 52 individuals.

Pressure (hPa)	Latitude (°N)		Estimate	SE	*z*	*p*
1000	37	Intercept	45.17	14.56	3.10	**0.002**
		Mean AGR	0.07	1.86	0.04	0.972
		Air temperature	0.25	0.32	0.79	0.431
		Departure date	-0.42	0.14	-3.02	**0.003**
925	37	Intercept	45.52	14.88	3.06	**0.002**
		Mean AGR	-0.23	2.00	-0.11	0.909
		Air temperature	0.23	0.23	1.01	0.315
		Departure date	-0.41	0.14	-3.01	**0.003**
850	37	Intercept	44.96	14.57	3.09	**0.002**
		Mean AGR	-1.11	2.30	-0.48	0.628
		Air temperature	-0.02	0.19	-0.10	0.922
		Departure date	-0.37	0.13	-2.83	**0.005**
1000	47	Intercept	47.72	14.58	3.27	**0.001**
		Mean AGR	1.07	2.36	0.45	0.650
		Air temperature	-0.26	0.34	-0.75	0.451
		Departure date	-0.40	0.13	-3.13	**0.002**
925	47	Intercept	47.72	14.71	3.24	**0.001**
		Mean AGR	1.18	2.41	0.49	0.624
		Air temperature	-0.14	0.20	-0.70	0.483
		Departure date	-0.41	0.13	-3.13	**0.002**
850	47	Intercept	46.54	14.27	3.26	**0.001**
		Mean AGR	-0.14	2.54	-0.06	0.955
		Air temperature	-0.12	0.16	-0.77	0.444
		Departure date	-0.39	0.13	-3.07	**0.002**

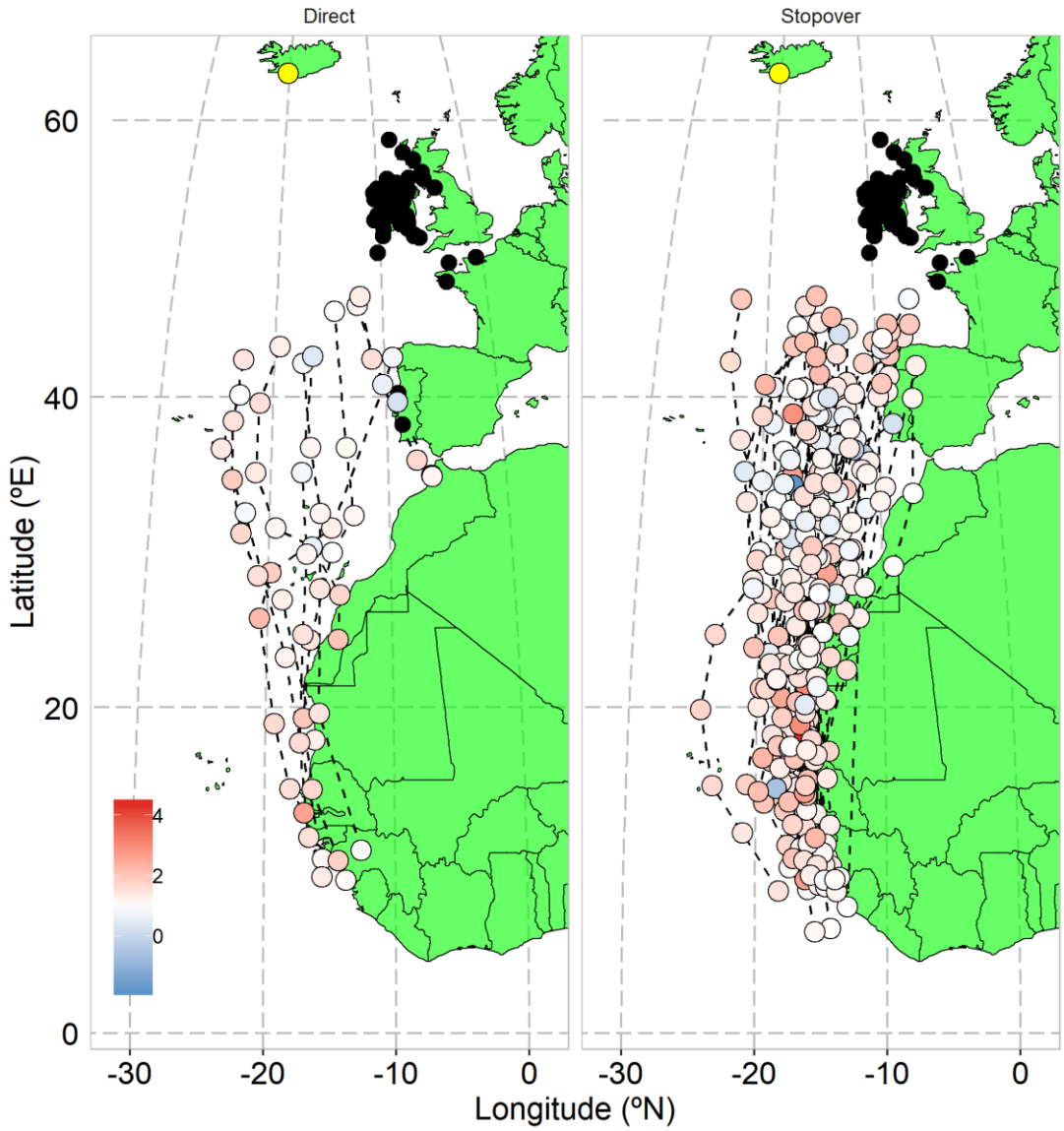

Figure A6.1.1. Spring migration locations recorded with geolocators up to latitude 47°N, coloured by air-to-ground speed ratio (at 1000 hPa; i.e. 111m above sea level); blue (values below one) represents wind support, whereas red (values above one) represents wind impediment in the direction of movement. Black dots depict stopover locations and the yellow dot marks the breeding site.

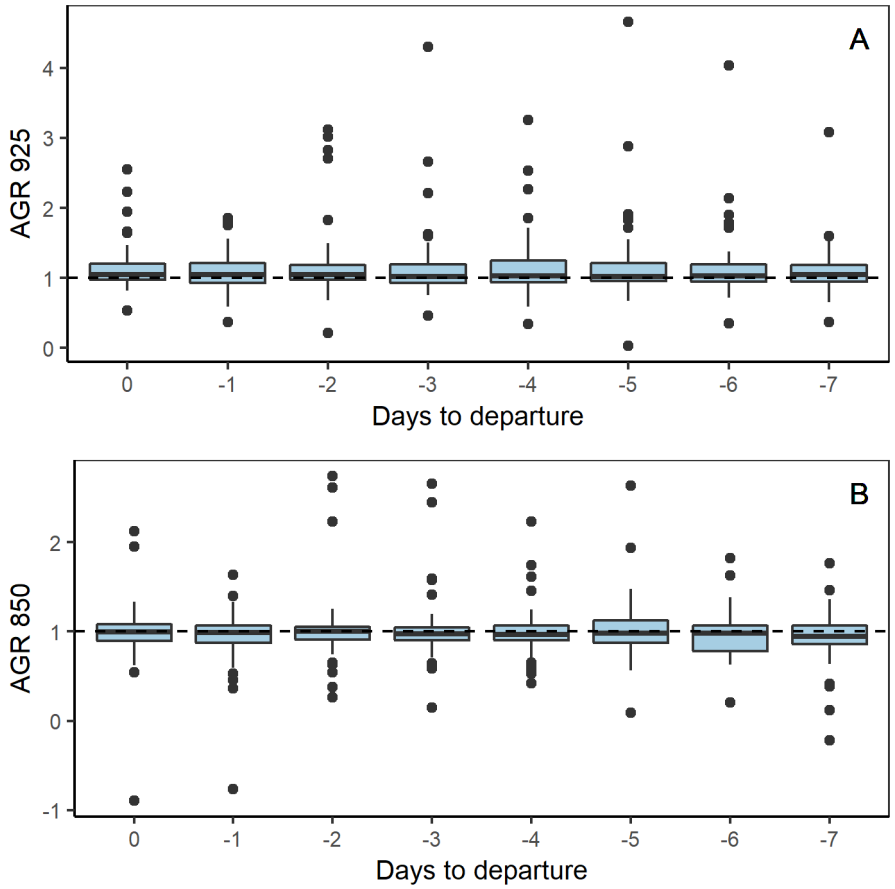

Figure A6.1.2. Air-to-ground speed ratio (AGR) at the time of departure (0) and at each 24h intervals prior to that time, for the air pressure of (A) 925 hPA (i.e. 762 m above sea level) and (B) 850 hPa (i.e. 1457 m above sea level); values below one represent wind support, while values above one mean impediment in the direction of movement. Boxplots show the median and 25 and 75% quartiles, whiskers extending up to 1.5 times the inter quartile range from the median and points beyond that are individually marked.

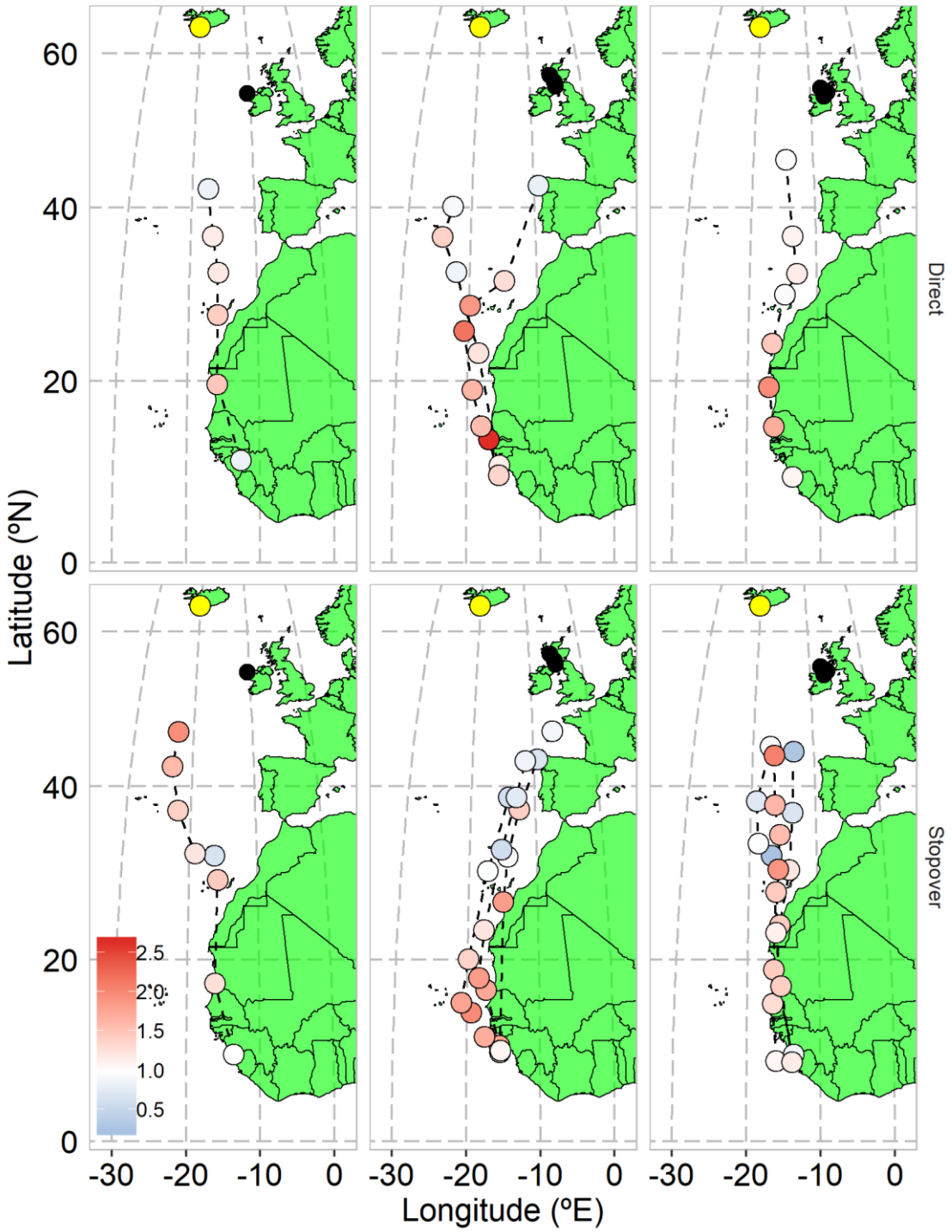

Figure A6.1.3. Spring migration locations recorded with geolocators up to latitude 47°N, coloured by air-to-ground speed ratio (at 1000 hPa; i.e. 111m above sea level), for three individuals that performed both direct and stopover strategies; blue (values below one) represents wind support, whereas red (values above one) represents wind impediment in the direction of movement. Black dots depict stopover locations and the yellow dot marks the breeding site.

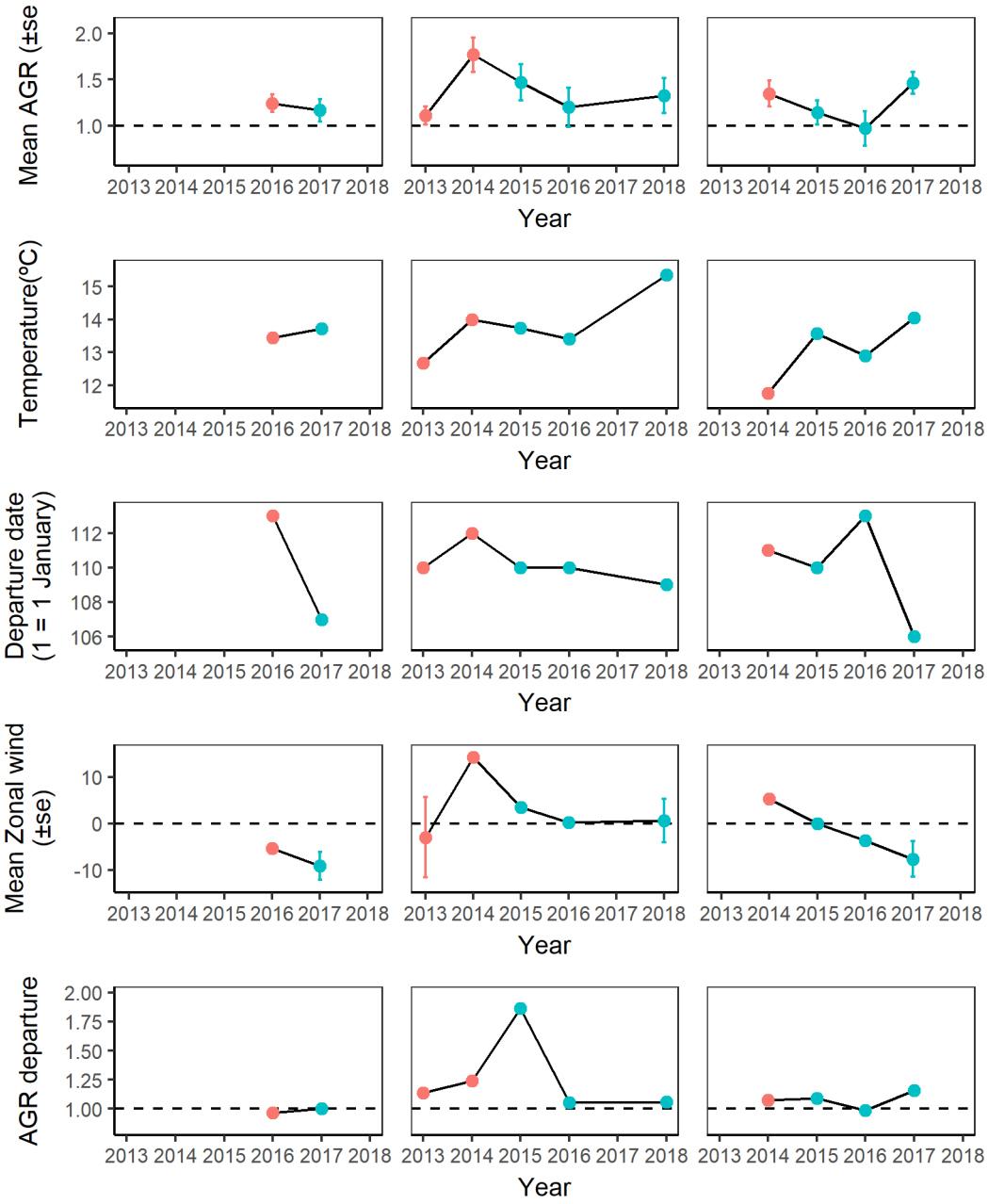

Figure A6.1.4. Individual level annual data of the three individuals that changed from direct (red) to stop-over (blue) strategy (top to bottom rows): mean air-to-ground speed ratio until 42°N, air temperature at 42°N, departure date in spring and average zonal wind experienced between 37 and 50°N.

CHAPTER 7

DISCUSSION

Previous photo by Tómas G. Gunnarsson.
Olé, Iceland, June 2015.
Whimbrels often defend their nest and chicks from arctic skuas.

DISCUSSION

Every year, Icelandic whimbrels bridge from the sub-arctic to the tropics and back, in flights of up to 6500 km. But what are the implications of these long-distance migrations for individual fitness?

The first step in tackling this question was establishing their migration routes and map the wintering and stopover ranges for this population (Chapter 2). Icelandic whimbrel wintering distribution extends from temperate to tropical regions along the east Atlantic coast in the northern hemisphere, and stopover locations are located mostly in Britain and Ireland. Contrary to most seasonal migrants (Nilsson et al. 2013), Icelandic whimbrels were shown to migrate faster during autumn than spring migration, as all individuals undertook a direct flight to the wintering areas, while in spring most (ca. 80%) made a stopover (Chapter 2). Among the proposed explanations for undertaking a stopover, were the possibility for individuals to assess weather conditions closer to the breeding sites, and that wind conditions would be unfavourable, thus preventing a direct flight also in this season. Both hypotheses are visited in Chapter 6.

A life-history trade-off was established between migration distance and wintering site quality, measured as energetic balance, among three wintering sites located at different climatic zones along Icelandic whimbrels' winter distribution. Individuals performing longer migrations spent the winter at more favourable sites (Chapter 3). It may be beneficial to spend the winter at sites where thermoregulatory costs are low and net energetic intake rate is high, because it might allow individuals to experience favourable conditions during moult and faster fuelling during spring migration. It was also established in Chapter 3 that fledging success decreases with laying date. Laying date, however, was not different among individuals wintering at different sites, nor was egg volume, suggesting no fitness consequences arising from variation in winter site quality (Chapter 3).

Given that winter location did not seem to influence laying date, flexibility and consistency in individual timing across the annual cycle were explored. Individuals were more consistent on timing of spring than autumn migration, and the most consistent stage during the annual cycle was spring departure date. This suggested some pressure to arrive on time at the breeding sites, given that earlier laying resulted in higher fledging success. Interestingly, timing of laying was the stage that varied the most (but only by an individual mean of 10 days, ± 0.8 SE), with no overall differences between sexes being apparent (Chapter 4). Such high individual consistency in phenology during the annual cycle may become disadvantageous given the current rate of climatic changes.

Individual timing consistency for a population with such wide distribution range and subjected to environmental stochasticity during several phases (e.g. migration or breeding), likely requires adjustment mechanisms when delays occur. Indeed, Icelandic whimbrels are capable of schedule adjustments during the annual cycle. In Chapter 5, I show a domino effect arising from autumn

migration departure date up to the following laying date. A series of correlations between those periods is evident, despite individuals' attempts to compensate delays at each stationary period. The duration at the wintering and stopover areas, and in the breeding grounds prior to laying, all decreased with arrival date at that location. Despite time compensation between consecutive annual stages is insufficient, the sum of time spent at all stationary periods since autumn departure until the following laying date allows individuals to compensate for delays between breeding seasons. Hence, Icelandic whimbrels can dissipate carry-over effects during the annual cycle and not incur fitness costs when delayed, which would be apparent in a delayed laying date.

Spring migration has substantial potential to create variation in individual timing just before the breeding season, as a direct strategy requires 4-5 days for completion since departure from the wintering site, whilst a stop-over strategy takes on average 10-25 days. As climate conditions can be of paramount importance for migration, I explored their role on spring migration of Icelandic whimbrels in Chapter 6. I show that the wind conditions experienced during migration were similar between strategies, and present evidence that a stopover may allow individuals to assess weather conditions in Iceland ahead of departure from the stopover site. Individuals undertaking direct flights to Iceland depart later from the wintering site and arrive considerably earlier than those performing a stopover strategy. Such early arrival, however, did not translate to early laying (Chapter 6).

As shown in several other systems (e.g. geese: Bêty et al. 2004; passerines: Norris et al. 2004; raptors: Sergio et al. 2007; waders: Alves et al. 2019), timing of breeding is also of paramount importance for Icelandic whimbrels, as fledging success tends to decrease with laying date (Figs. 3.4C and 5.2H). But what other processes may influence timing of laying in this population?

Drivers of timing of laying

No influence of wintering location or spring migratory strategy on laying date was detected (Chapters 3 and 6). The date of arrival to Iceland, however, had a significant positive effect on laying date (which, in turn, can be influenced by previous annual events; Chapter 5), as earlier arriving individuals tend to lay earlier. But laying date can also depend on other factors, such as food supply, weather conditions and pair bond. Food supply has long been a known important driver of the timing of breeding (Perrins 1970, Drent 2006), and in several experiments in which individuals were provided supplementary food laying date advanced (Drent 2006, Ruffino et al. 2014). For example, food supplemented groups (twice daily) of Florida scrub jays *Aphelocoma coerulescens* advanced the laying date on average by 16 days, compared to control groups (Schoech 1996). Weather conditions, such as temperature, have also been shown to have an effect on laying date (Dunn 2004, Kwon et al. 2017, Drake and Martin 2018, Alves et al. 2019), although its effect through food supply might be difficult to tease apart. In monogamous mating systems, maintaining the pair bond can also be advantageous. For example, in blue-footed boobies *Sula nebouxii* newly formed pairs tended to lay considerably later than pairs in their second year together (Sanchez-Macouzet et al. 2014).

There is no detailed data on whimbrel food supply prior to laying, in order to explore its effect on laying date. However, the influence of a pair bond can be explored, as several birds have been marked in the course of this study and their nesting parameters recorded over several years. After arrival, individuals wait for the partner (difference of spring arrival date within pairs that maintained the bond: 5.3 days ± 0.7 SE, n = 15). If the partner fails to arrive, or does not arrive within a given period of time, a divorce might occur (Gunnarsson et al. 2004) and mate sampling and forming a new bond should require some additional time. In fact, there seems to be a slight tendency for whimbrels to lay earlier when they maintain the pair bond, compared to when a new pair bond is created (Fig 7.1A), And when the pair bond is maintained, laying date shows a tendency to advance in relation to the previous year, by an average of 2.48 days (±1.47, SE; Fig. 7.1B). By estimating the probability of a whimbrel to maintain the mate in relation to the previous year (62.4%; n = 157), it is possible to estimate the trend of laying date during an individual's reproductive period. Assuming a reproductive period of eight years, a whimbrel would maintain the partner for 4.99 breeding seasons (i.e. 0.624 * 8) and mate with a new one in 3.01 of them (i.e. 0.376 * 8). This would result in an overall advancement of 11.06 days (advancement of 12.38 days, i.e. 4.99 * 2.48, minus delay of 1.32 days, i.e. 3.01 * 0.44). Hence, it seems that whimbrels tend to advance laying date with age, but these estimates must be interpreted with caution, given the variation around the mean of laying shift (SE = 1.47 days for mate-retention; Fig. 7.1B). Nevertheless, to maintain or find a new mate seems to explain part of the individual range of laying dates (Chapter 4).

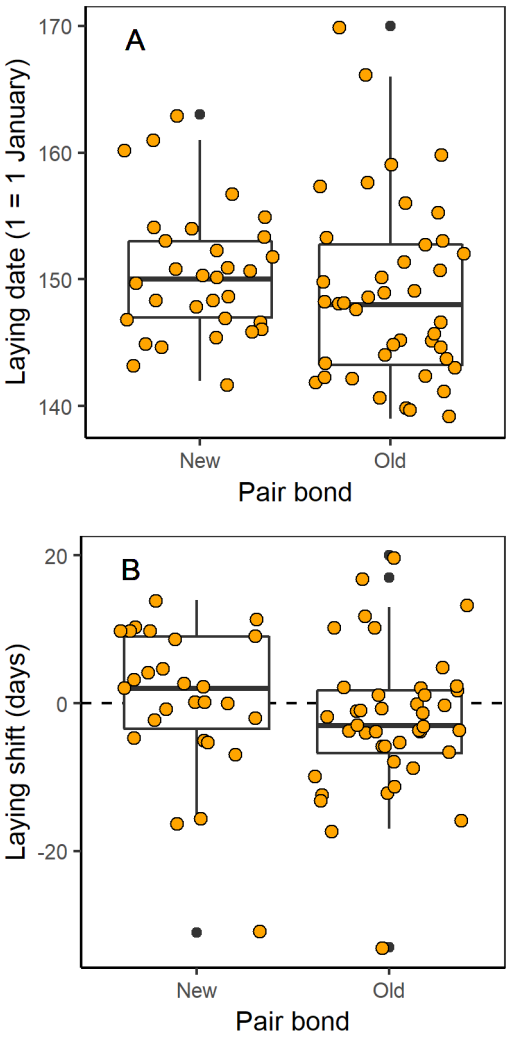

Figure 7.1. Variation in (A) laying date and (B) laying date shift, in relation to previous year, for individuals that maintained (Old; n = 42) or formed a new pair bond (New; n = 31), in relation to the mate from the previous year. Known replacement clutches were excluded. No statistical differences were found (Mann-Whitney-Wilcoxon test: (A) W = 792.5, p = 0.1149; (B) W = 715.5, p = 0.06837). Boxes show the median and 25 and 75% quartiles, whiskers extend up to 1.5 times the inter quartile range from the median and points beyond that are individually marked in black; each circle represents one pair.

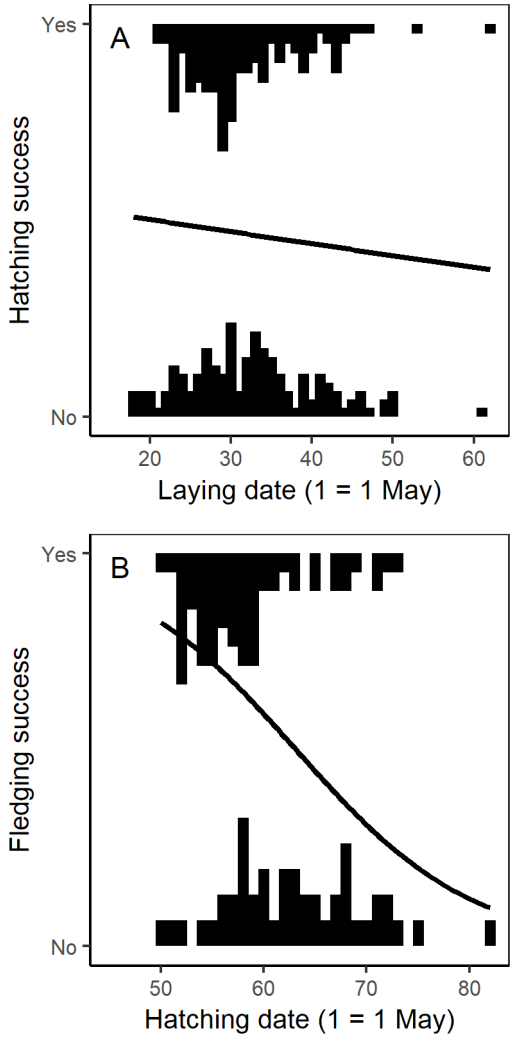

Figure 7.2. Logistic curves of (A) hatching success in function of laying date and (B) fledging success in function of hatching date.

Table 7.1. Logistic regressions testing the effect of (A) laying date and year on hatching success and (B) hatching date and year on fledging success; estimates for year are in relation to 2015.

		Estimate	SE	z	*p*
A	Intercept	0.30	0.60	0.51	0.614
n = 258	Laying date	-0.01	0.02	-0.74	0.461
Hatching	Year 2016	-0.12	0.33	-0.35	0.723
success	Year 2017	-0.03	0.33	-0.08	0.935
B	Intercept	7.91	2.26	3.50	**<0.001**
n = 109	Hatching date	-0.12	0.04	-3.46	**<0.001**
Fledging	Year 2016	-0.16	0.55	-0.29	0.774
success	Year 2017	-0.31	0.55	-0.57	0.569

Why does fledging success decrease with laying date?

The pattern of decreasing fledging success with laying date may arise during two periods: nesting and chick rearing. First, a differential nest predation rate, where later nests suffer higher predation, would naturally depress fledging success with laying date, while assuming an even predation pressure on broods. Second, the trend of fledging success may only appear after hatching, with more chicks perishing the later they hatched. In fact, hatching success does not vary significantly with laying date (Fig. 7.2A; Table 7.1A), but fledging success decreases with hatching date in a similar fashion as it decreases with laying date (Fig 3.4C; Fig. 7.2B, Table 7.1B), supporting that the trend is established during chick rearing.

After hatching, whimbrel chicks leave the nest and start foraging under the protection of their parents. There are three non-mutually exclusive processes through which chicks may not fledge: food depletion throughout the season, an increase in predation pressure and adult quality. Food resources are an important driver of breeding success (Perrins 1970, Drent 2006) and can limit chick growth and survival (Pearce-Higgins and Yalden 2004, Both et al. 2006, McKinnon et al. 2012). Although there is no detailed information on the diet of Icelandic whimbrel chicks, it is known that they consume surface dwelling arthropods (Gudmundsson 1957, Gunnarsson 2000). During this study, twelve pitfalls traps were set in Icelandic whimbrel breeding areas, between mid-May and mid-August, and emptied weekly, although some traps were destroyed by cattle in some weeks. The data

collected shows no consistent seasonal variation among years. However, at the same time, fledging success consistently decreased throughout the season (Fig 7.3). Additionally, whimbrel chick growth was recorded and the growth curve of early and late hatching chicks (in relation to the mean) was similar (Fig. 7.4), suggesting that food supply is unlikely to limit chick survival.

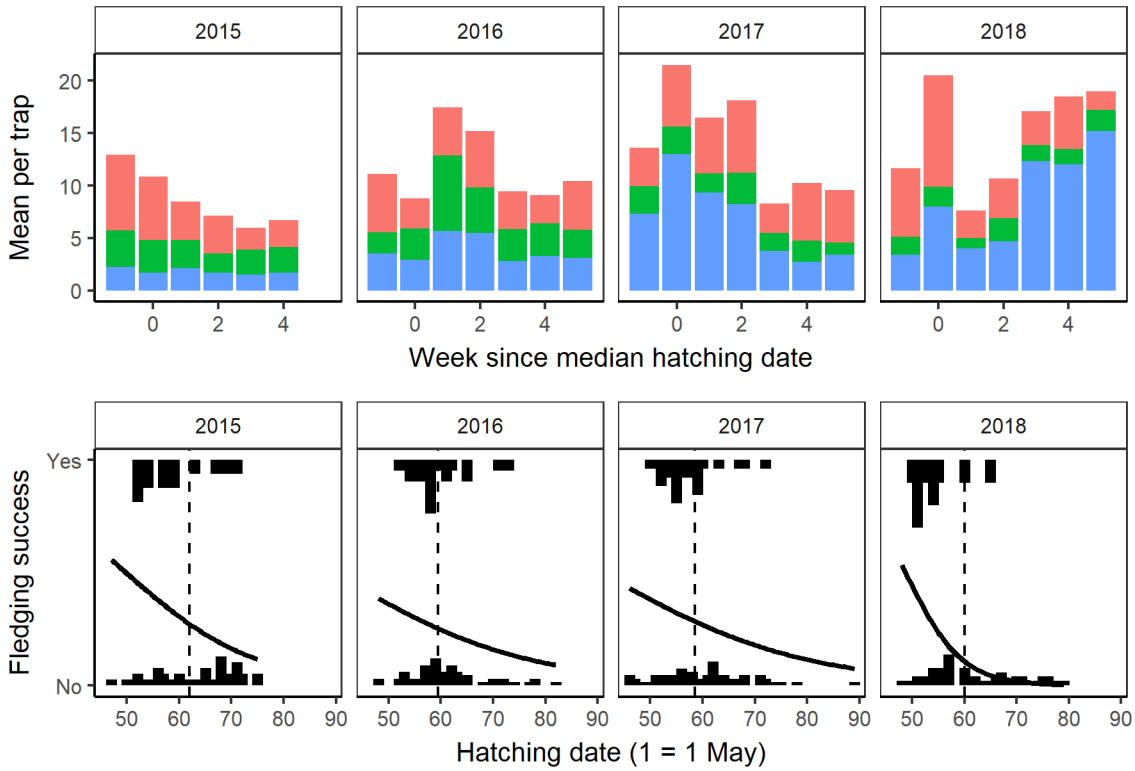

Figure 7.3. Variation on: (top row) mean quantity of prey items per pitfall trap/week (6-12 traps) since median hatching date, between 2015 and 2018, coloured by prey type (blue: Opiliones; green: Coleoptera; orange: Araneae); and (bottom row) fledging success in function of hatch date each year, for the same period as above plots; dashed lines mark the median laying date.

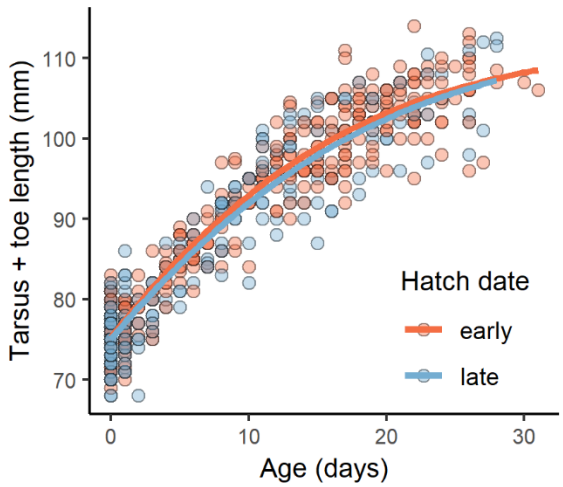

Figure 7.4. Growth rates of chicks that hatched before (early; red) of after (late; blue) the mean hatching date of the year; lines depict fitted logistic growth curves.

Whimbrel nests are predated by a suite of natural and livestock species, such as arctic foxes *Vulpes lagopus*, arctic skuas *Stercorarius parasiticus*, ravens *Corvus corax*, sheep and horses (Katrínardóttir 2012; pers. obs.). Data on Icelandic whimbrel chick predators has not been systematically recorded, but arctic skuas and ravens are common in whimbrel breeding areas and have been observed predating on chicks (pers. obs.). Ravens have been seen, in what seemed to be family groups, observing whimbrel families (and maybe of other species), apparently waiting for chicks to break cover and be spotted (pers. obs.). These and other predators are not specialised on whimbrel chicks, thus variation in predation pressure at the (wader) community level could explain the decline of whimbrels' fledging success through the season. Oystercatchers *Haematopus ostralegus*, golden plovers *Pluvialis apricaria*, redshanks *Tringa totanus* and common snipes *Gallinago gallinago* share breeding sites with whimbrels, so predators have considerable supply of wader chicks as soon as whimbrel hatching starts. However, chicks of all these species start hatching earlier than whimbrels (Gunnarsson, unpublished), which could mean that late hatching whimbrels will have a higher predation pressure than early ones, as not only fewer whimbrels chicks are around later in the season but also fewer wader chicks. In addition, all those waders are advancing their spring arrival dates, and likely their breeding timing, whereas whimbrels are not (Chapter 4; Gunnarsson and Tómasson 2011).This may lead to a steeper negative relationship between laying date and fledging success in the future.

Parental quality may also play a role in the seasonally decreasing fledging success and it may interact with predation pressure. This thesis established that Icelandic whimbrels are consistent in their timing, including laying date (Chapter 4), which suggests that early birds are of higher quality, since they are more likely to consistently fledge young (Sydeman and Eddy 1995). If quality is also expressed in anti-predator behaviour, then early laying birds may be more likely to better protect their brood and successfully fledge young.

Long-term fitness and population implications

Although differences in breeding success are evident in one season, whimbrels are long-lived birds, which may allow the opportunity to attenuate the effect of breeding failures in a particular breeding season (e.g. due to predation stochasticity), over their lifetime. Nevertheless, the lifetime reproductive success of Icelandic whimbrels is likely to differ depending on individual schedule, because an early bird will be consistently early and thus experience higher chances of being successful each season, compared to a late conspecific. By being early, not only might fledging success be higher, but those fledglings may also be more likely to recruit (van de Pol et al. 2006, Alves et al. 2019) and breed similarly early as their parents, since this trait can have a hereditary component (Merilä and Sheldon 2001). Hence, timing of breeding can affect population dynamics, through variation in recruitment probability of individuals produced throughout the season.

This thesis established that whimbrels are highly consistent. But individual consistency may be disadvantageous in a scenario of fast climatic changes. In Iceland, most species of waders have been advancing their spring arrival dates in parallel to the increasing temperature trend in the country, but whimbrels have not (Chapter 4; Gunnarsson and Tómasson 2011, Gill et al. 2014). Yet, at the same time there is no indication of a population decline (Skarphéðinsson et al. 2016). Whimbrels are one of the latest waders to arrive to Iceland and have a relatively short breeding period, compared to other wader species breeding in the same area (Gunnarsson, unpublished data). The length of the period with available minimum resources for breeding of Icelandic whimbrels remains unknown. But if it is wider than required for successful breeding, it could be that whimbrel have been reproducing within that window, even while environmental conditions are advancing. However, under continuous advancement of spring conditions, consistency might prevent individuals from responding to changes when time windows mismatch, with peak resource availability becoming considerably earlier than peak resource demand (Both et al. 2006, Kwon et al. 2019). At such a hypothetical point it may be expected that whimbrel recruits alter the species phenology, assuming a new schedule and presenting a population level response to environmental changes, similarly to what was observed in Icelandic black-tailed godwits (Gill et al. 2014).

The long term phenological pattern of arthropod abundance in Iceland is unknown, but given the changes in spring temperature, this group might have advanced, similarly to what has been recorded in other wader breeding locations: Siberia (Tulp and Schekkerman 2008) and Greenland (Reneerkens et al. 2016). Forecasting a trophic mismatch scenario, it could be expected that late hatching chicks would be less likely to find enough arthropods and thus grow slower than earlier hatched chicks, but that does not seem to be the case (Fig. 7.4). Therefore, food supply does not seem to be limiting for whimbrel chicks' development and survival in Iceland. In the breeding grounds, crowberry *Empetrum nigrum* are abundant, and remains of the fruit are commonly found in chicks and adult droppings, suggesting it might be an important food supply. This plant species is reported to have advanced fruiting phenology in the Netherlands, while it also increased in biomass and extend the growing season by 75 days in response to warming temperatures (Buizer et al. 2012). The situation in Iceland is unknown, but if a similar response has occurred, crowberries may buffer potential negative effects of an advancing arthropod phenology and associated tropic mismatch (Fig. 7.5). This could result in limited selection pressure on whimbrels to advance their phenology and potentially explain the stable population size (Skarphéðinsson et al. 2016) and arrival dates (Fig 4.1). In fact, the phenology of Icelandic whimbrels has likely been stable for a very long time, as in the late 1950's Finnur Gudmundsson (1957) described their spring phenology exactly as it occurs today: "*In spring the whimbrels arrive in the last third of April and the first half of May*".

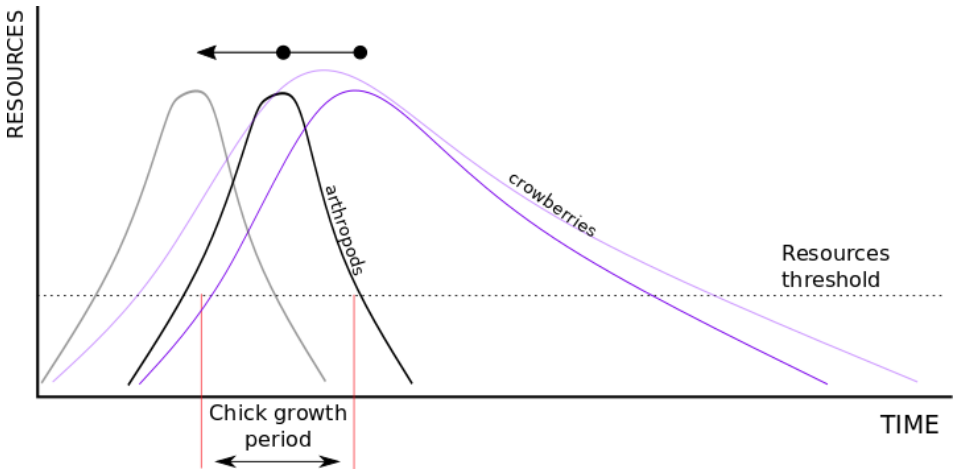

Figure 7.5. Hypothetical scenario of changes in phenology of food resources: arthropods (in black) and crowberries (in purple). Lighter colours represent the current situation, when the period of chick growth is mismatched with advancing arthropod peak but increasingly matched to crowberries, which have likely advanced and widened its phenology, and increased in abundance.

Having determined the importance of timing of events in the annual cycle on Icelandic whimbrel fitness and explored several factors that can influence it, it is now important to acquire knowledge on resource dynamics in the breeding areas and on the ontogeny of migration and associated timing. Several questions remain to be answered regarding the trophic relationships of Icelandic whimbrels and their prey, such as the exact importance of each prey type for chicks' growth, but also which food resources fuels the +6000 km flight in autumn. Crowberries are likely to be very important, hence a detailed investigation of the consumption of these fruits by birds, together with a seasonal and annual monitoring of its phenology and abundance shall enlighten why are Icelandic whimbrels apparently stable in population size and phenology, while (most) environmental conditions are changing. The response of adults to a changing environment seems limited, given their timing consistency during the annual cycle, but transgenerational changes in individual phenology can explain population level responses. Hence it is important to study how juveniles define their migratory schedules (e.g. is it influenced by hatching date, parental schedule, social cues or other processes), and what factors may limit their recruitment. Such knowledge will undoubtedly contribute to our current understanding of population-level responses of long-distance migrants to environmental change.

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Supplementary Material

Two supplementary outputs were produced during the work developed for this thesis. First, while collecting data on whimbrels foraging behaviour in the Banc d'Arguin, birds were recorded consuming West African Bloody Cockles *Senilia senilis,* a behaviour previously undescribed. Second, after conducting the methods in Chapter 3, a package was developed for R software, that simplifies the process of estimating the thermoregulation costs and maintenance metabolism of waders. These two outputs are presented here.

Previous photo by Camilo Carneiro.
Whimbrel food, Guinea-Bissau, 24 January 2016.
Fiddler crab is the main prey of whimbrels in the Bijagós Archipelago.

BLOODY COCKLES: A NOVEL AND IMPORTANT FOOD ITEM FOR WHIMBRELS IN THE BANC D'ARGUIN

Camilo Carneiro, Tómas G. Gunnarsson, José A. Alves

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The Banc d'Arguin, in Mauritania, is one of the three most important areas for wintering waders along the East Atlantic Flyway (Araujo & Campredon 2016), and where over 30000 Whimbrels *Numenius phaeopus* were counted in the winter 1999-2000 (Hagemeijer *et al.* 2004), originating from NE and NW Europe (i.e. *N. p. phaeopus* and *N. p. islandicus*; BWPi 2006, Gunnarsson & Guðmundsson 2016). In the mid-1980s, wintering Whimbrels in the Banc d'Arguin displayed a diet solely comprised of crabs (Fiddler *Uca tangeri*, Blue *Callinectes marginatus* and African Mud *Panopeus africanus*; Zwarts & Dirksen 1990). In January and February of 2017, the same areas studied by Zwarts & Dirksen (1990) 30 years ago (located on the west side of Baie d'Aouatif; 19°54' N, 16°17' W) were visited and Whimbrels were recorded eating crabs, but also West African Bloody Cockles *Senilia senilis* (hereafter Bloody Cockles), a behaviour thus far not described in the bibliography.

In the mid-1980s, Bloody Cockles were absent from the area studied by Zwarts & Dirksen (1990; Theunis Piersma & Leo Zwarts pers. comm.), but Whimbrels were also not observed foraging on them elsewhere in the Banc d'Arguin (Leo Zwarts pers. comm.). Currently, Bloody Cockles are found almost everywhere in the study area (Fig. 1), and their total biomass in the region has increased 10-fold from the 1980s to 2000s (Honkoop *et al.* 2008).

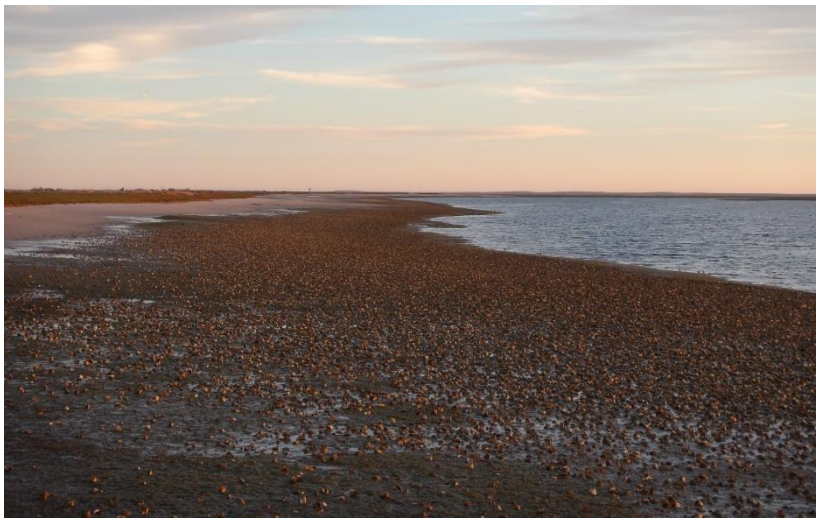

Figure 1. Beach on the west of side of Baie d'Aouatif, Banc d'Arguin, Mauritania, at low tide (29 Jan 2017). This extensive West African Bloody Cockle bed, composed of many empty shells but also live individuals, was nonexistent in the mid-1980s (Theunis Piersma & Leo Zwarts pers. comm.). Photo: Camilo Carneiro.

Figure 2. Whimbrel pulling the flesh out of a West African Bloody Cockle in Banc d'Arguin, Mauritania (9 Feb 2017). Photo: Camilo Carneiro.

Bloody Cockles can grow over 9 cm in length and are buried at shallow depths in the sediment, sometimes emerging slightly (Wolff *et al.* 1987, Swennen 1990). Whimbrels were observed inserting the bill in the open bivalve and pull out the flesh (Fig. 2). While doing so, sometimes the entire bivalve was unearthed and, in such cases, it was shaken until the flesh was detached from the shell. Although occasionally a large portion of flesh was removed at once and ingested, most frequently Whimbrels consumed the flesh in small portions. The flesh was sometimes washed in nearby water and occasionally discarded after washing.

Oystercatchers *Haematopus ostralegus* are the main avian predator of Bloody Cockles in the Banc d'Arguin (Swennen 1990), as Oystercatchers are able to stab them and remove the flesh for consumption. Whimbrels were not recorded stabbing Bloody Cockles, but on some occasions seemed to peck them and pull the flesh quickly. It is likely that they were eating dead or weak and dying cockles that were unable to close their shells, or do so rapidly. This is also supported by the fact that Whimbrels were not hitting the bivalves with fast movements, and thus were likely aware of a low potential low risk of the cockle closing its shell while the bill was still inserted. Furthermore, the observations of Whimbrels sometimes discarding the bivalve's flesh after investing time into pulling and washing it also suggests that the cockle was dead and possibly decomposing, being then considered unsuitable for consumption.

One minute focal observations (n = 519) were performed on foraging Whimbrels and in 12.5% of the focal periods, flesh of Bloody Cockles was consumed. Complementary observations of handling time (time from finding to swallowing prey) were also conducted and on average 1.6 ± 1.4 (mean ± SD) mins were required for Whimbrels to handle Bloody Cockles (range: 0.1 - 6.2 mins, n = 22). This substantial time investment suggests a relatively high value of this prey. Additionally, the flesh ingested is mostly composed of organic matter, unlike crabs, which about half its mass is composed of inorganic material and have lower digestibility (Zwarts & Blomert 1990). For these reasons, the now-abundant Bloody Cockles may currently be an important prey for wintering Whimbrels in the Banc d'Arguin and should therefore be taken into account when studying the species' diet.

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eneRgetics - ESTIMATING THERMOREGULATION AND MAINTENANCE METABOLISM OF SHOREBIRDS IN R

Camilo Carneiro, Ricardo Correia, José A. Alves

After conducting the methods in Chapter 3, a package was developed for R – eneRgetics – that simplifies the process of estimating the thermoregulation costs and maintenance metabolism of waders, following the model established by Wiersma & Piersma (1994). It provides functions to: (i) retrieve the necessary environmental data from web sources to calculate the maintenance metabolism; (ii) retrieve tidal data from online resources (often useful, given many shorebirds move between microhabitats in accordance with the tidal cycle; and to classify tide states in relation to low tide. Given that thermoregulation only incurs costs when maintenance metabolism is higher than the Basal Metabolic Rate, it also provides (iii) a function to calculate this, following Kersten & Piersma (1987) and Kersten et al. (1998).

Although not yet published, this package can be found at https://github.com/CamiloCarneiro/eneRgetics.

The following explanatory exercise (also presented in the package's vignette) exemplifies how to use the functions in *eneRgetics*.

Explanatory exercise

Imagine we want to estimate the maintenance metabolism of the Whimbrel (*Numenius phaeopus*) for a period of time during the non-breeding season of 2016-2017 in the Banc d'Arguin, Mauritania (latitude N 19.9, longitude W 16.3). Let's assume that period to be from 7 to 14 January 2017. During the non-breeding season whimbrels usually forage in intertidal areas at low tide and during high tide roost in flocks above the high tidemark. Hence, their microhabitat use will vary in relation to the tide (*e.g.* being in open tidal flats while foraging and roosting in less exposed habitats the rest of the time).

We need the following data to calculate their maintenance metabolism:
I. Time budget: the proportion of time spent at each microhabitat per tide state (*e.g.* at each hour in relation to low tide; microhabitats from Wiersma & Piersma (1994));
II. Weather: temperature, wind, solar irradiance;
III. Tide table;
IV. Whimbrel body mass and breast height.

1. Field data

First we need to know how much time whimbrels spend on each microhabitat. Microhabitat use is related to their activity (*e.g.* foraging during low tide in open tidal flats or roosting during high tide). To do so, we have recorded the percentage of birds on each activity, at given time intervals - in this case the proportion of birds roosting and not roosting (*i.e.* foraging, preening, interacting) - over the course of the non-breeding season. We end up with the following type of data:

```
head(time_budget)
```

date	time	perc_roosting	perc_not_roosting
05-01-2017	08:25	0.27	0.73
05-01-2017	08:45	0.36	0.64
05-01-2017	09:15	0.74	0.26
05-01-2017	09:30	0.86	0.14
05-01-2017	09:45	0.87	0.13
05-01-2017	10:00	0.62	0.38

2. Summarising data

Following Altmann (1974), we assume that the average percentage of individuals in a given activity during an interval is similar to the amount of time an average individual spends on that activity in the same interval. Hence, we now need to summarise all our observations in order to calculate the average time spent on each activity and, consequently, on each microhabitat. Given that whimbrels follow a tidal cycle, we will do so in relation to the tidal state. Using `tidal_codes()` we can calculate the time to the nearest low tide for each observation and then use those codes to summarise the data. In order to do so, we need a tide table for our study location and for the period of the observations. This can be obtained using `get_tides()`.

```
# note that `tidal_codes()` requires that our data has datetime stamp in
POSIXct with time zone information

time_budget$date <- as.POSIXct(paste(time_budget$date, time_budget$time),
 format = "%Y-%m-%d %H:%M", tz = "GMT")


time_budget <- time_budget[, -2] #remove column 'time'


head(time_budget)
```

date	perc_roosting	perc_not_roosting
05-01-2017 08:25	0.27	0.73
05-01-2017 08:45	0.36	0.64
05-01-2017 09:15	0.74	0.26
05-01-2017 09:30	0.86	0.14
05-01-2017 09:45	0.87	0.13
05-01-2017 10:00	0.62	0.38

The observations were made between 2017-01-05 and 2017-02-01 in order to represent the non-breeding behaviour/microhabitat use, so we will retrieve tidal data for the same period.

```
latitude <- 19.9
longitude <- -16.3
start <- "2017-01-05"
end<-"2017-02-01"
time_zone <- "GMT"
key <- "write_worldtides_key_here"


tides_jan <- get_tides(lat = latitude, lon = longitude, start_date = star
t, end_date = end, tzone = time_zone, API_key = key)
```

To create the tide codes, we run:

```
time_budget_with_code <- tidal_codes(time_budget, tides_jan)
```

And we get the previous data frame with the additional *tide_code* column (*i.e.* the time to the nearest low tide in hours):

```
head(time_budget_with_code)
```

date	perc_roosting	perc_non_roosting	tide_code
05-01-2017 08:25	0.27	0.73	-4
05-01-2017 08:45	0.36	0.64	-4
05-01-2017 09:15	0.74	0.26	-3
05-01-2017 09:30	0.86	0.14	-3
05-01-2017 09:45	0.87	0.13	-3
05-01-2017 10:00	0.62	0.38	-2

There are many ways to summarise the data. Here we use the `dplyr` package.

```
require(dplyr)
summary_data <- time_budget_with_code %>%
  group_by(tide_code) %>%
  summarise(n_observations = length(tide_code),
            mean_roosting  = mean(perc_roosting, na.rm = T),
            mean_not_roosting  = mean(perc_not_roosting, na.rm = T))
```

tide_code	n_observations	mean_roosting	mean_non_roosting
-6	29	0.860345	0.139655
-5	52	0.638846	0.361154
-4	59	0.433390	0.566610
-3	51	0.271569	0.728431
-2	44	0.192046	0.807955
-1	40	0.169500	0.830500

Now we know the proportion of time that the Whimbrel spend, on average, in each microhabitat at hourly intervals in relation to the tide.

3. Retrieving weather data

To calculate the maintenance metabolism we need weather data (namely air temperature, wind speed and solar irradiation). Using `get_weather()` we can retrieve such data from the web (see function details for more info).

```
cams_user <- "write_email@here.com"
API_key <- "write_darksky_API_key_here"
latitude <- 19.9
longitude <- -16.3
start_date <- "2017-01-07"
end_date<-"2017-01-14"
reli_score <- 0.5
time_zone <- "GMT"


weather_jan <- get_weather(lat = latitude, lon = longitude, start_date =
start_date, end_date = end_date, tzone = time_zone, reli_score = reli_sco
re, API_key = API_key, cams_user = cams_user)
```

We get a data frame with the following structure:

```
head(weather_jan)
```

date	temperature	wind_speed	GHI
07-01-2017 00:00	17.78	3.58	0
07-01-2017 01:00	17.22	3.58	0
07-01-2017 02:00	17.22	4.02	0
07-01-2017 03:00	16.11	3.13	0
07-01-2017 04:00	16.11	2.68	0
07-01-2017 05:00	17.22	2.68	0

4. Calculating maintenance metabolism

Now we have all the required input to calculate the hourly maintenance metabolism (*m_maint*). Following Wiersma and Piersma (1994), we assume the microhabitats used during roosting and not roosting periods were h8 (Open group) and h3 (Mudflat and bare salt marsh), respectively, and therefore use the respective habitat specific formulae. Note that other microhabitats are available in order to accommodate different microhabitat use. The time budget data frame needs to be formatted accordingly to be used by `mmaint()`. Given that thermoregulation costs only occur when *m_maint* is higher than BMR, if BMR is calculated beforehand (or present in the R environment) the plot produced by `mmaint()` shows it as a horizontal line. The plot shows the initial 360 data points (ca. 15 days) in the dataset and prints the range of *m_maint* values, in order to allow an assessment of the results produced.

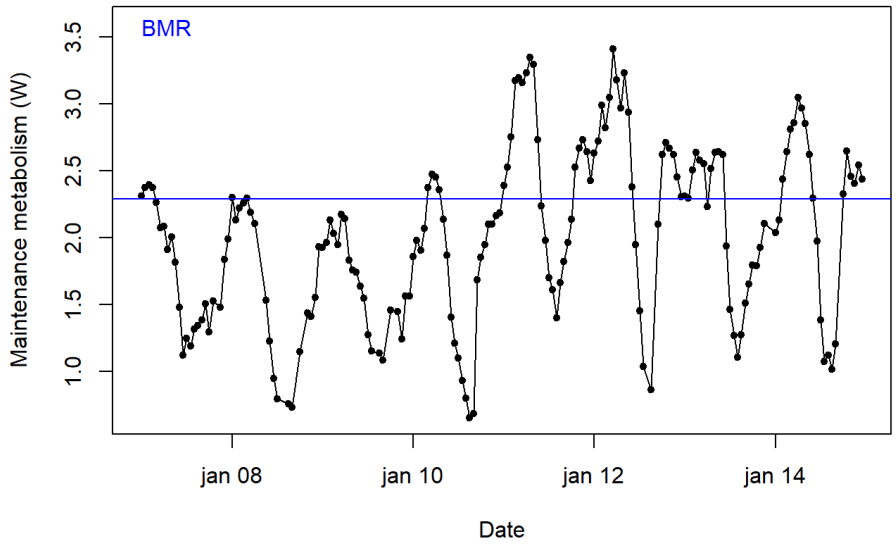
```
# preparing the time budget data frame
names(summary_data)[names(summary_data) == "mean_not_roosting"] <- "h3"
names(summary_data)[names(summary_data) == "mean_roosting"] <- "h8"

summary_data <- summary_data[,c("tide_code","h3","h8")]

# calulating BMR
body_mass <- 460
region <- "trop"

BMR<-bmr(body_mass = body_mass, region = region)

# calculating maintenance metabolism
weatherData <- weather_jan
tide_table <- tides_jan
time_budget <- summary_data
```

```
breast_height <- 0.17


Maintenance_metabolism <- mmaint(weatherData = weatherData, tide_table =
tide_table, timeBudget = time_budget, breast_height = breast_height, body
_mass = body_mass)

head(Maintenance_metabolism)
```

tide_code	date	temperature	wind_speed	GHI	h3
-6	08-01-2017 10:00	20.00	0.89	348.7451	0.1396552
-6	14-01-2017 03:00	17.22	8.94	0	0.1396552
-6	12-01-2017 01:00	17.22	9.83	0	0.1396552
-6	09-01-2017 11:00	22.22	4.47	206.6119	0.1396552
-6	07-01-2017 21:00	21.11	0.89	0	0.1396552
-6	07-01-2017 09:00	17.78	3.13	208.4848	0.1396552

h8	h1	h2	h4	h5	h6	h7	h9	h10	h11	m_maint
0.8603448	0	0	0	0	0	0	0	0	0	1.225394
0.8603448	0	0	0	0	0	0	0	0	0	2.643775
0.8603448	0	0	0	0	0	0	0	0	0	2.722218
0.8603448	0	0	0	0	0	0	0	0	0	1.547975
0.8603448	0	0	0	0	0	0	0	0	0	1.479549
0.8603448	0	0	0	0	0	0	0	0	0	1.814515

```
## [1] "m_maint range: 0.651 - 3.41"
```



5. What if microhabitat use does not vary according to tides?

Suppose the Whimbrel do not vary on the microhabitat use in relation to the tidal rhythm but that their use of each microhabitat is constant each day, as the following:

```
time_budget_no_tides
```

```
##     h3   h8
## 1 0.58 0.42
```

In such case, we provide that information to `mmaint()`, with no tide_table argument:

```
weatherData <- weather_jan

time_budget <- time_budget_no_tides

breast_height <- 0.17

body_mass <- 460


Maintenance_no_tides <- mmaint(weatherData = weatherData, timeBudget = ti
me_budget, breast_height = breast_height, body_mass = body_mass)

head(Maintenance_no_tides)
```

date	temperature	wind_speed	GHI	h1	h2	h3	h4	h5	h6	h7
07-01-2017 00:00	17.78	3.58	0	0	0	0.58	0	0	0	0
07-01-2017 01:00	17.22	3.58	0	0	0	0.58	0	0	0	0
07-01-2017 02:00	17.22	4.02	0	0	0	0.58	0	0	0	0
07-01-2017 03:00	16.11	3.13	0	0	0	0.58	0	0	0	0
07-01-2017 04:00	16.11	2.68	0	0	0	0.58	0	0	0	0
07-01-2017 05:00	17.22	2.68	0	0	0	0.58	0	0	0	0

h8	h9	h10	h11	m_maint
0.42	0	0	0	2.227418
0.42	0	0	0	2.281137
0.42	0	0	0	2.344780
0.42	0	0	0	2.317329
0.42	0	0	0	2.244460
0.42	0	0	0	2.144366

6. Important note

In the current version, the geographical coverage of `get_weather()` is spatially restricted to -66 and 66 degrees latitude and longitude, and has a temporal coverage starting in 2004-02-01 and ending 2 days prior to the data retrieval.

7. References

Altmann, J. 1974. Observational Study of Behavior: Sampling. - Behaviour 49: 227-267.

Kersten, M., Bruinzeel, L., Wiersma, P. & Piersma, T. 1998. Reduced basal metabolic rate of migratory waders wintering in coastal Africa. - Ardea 86: 71-80.

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Wiersma, P. and Piersma, T. 1994. Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of red knots. - Condor 96: 257 - 279.